ABSTRACT

Title of Dissertation: PLANT–ARTHROPOD ASSOCIATIONS FROM THE WESTERN INTERIOR OF NORTH AMERICA DURING THE LATE CRETACEOUS

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Doctor of Philosophy, 2020

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Insects are unparalleled in species diversity and breadth of ecological associations. The most prominent of these ecological associations is insect herbivory on vascular plants, which has shaped terrestrial ecosystems for hundreds of millions of years. Only recently have scientists begun to understand the diversity and intensity of plant–insect associations in the fossil record. The majority of these studies have documented episodes of rapid change in Earth's history, such as intervals of global warming. However, there are few studies documenting plant–insect associations around longer time intervals, including the radiation of flowering plants (angiosperms) during the Cretaceous Period from 145 to 66 Ma (Mega-annum),

which set the stage for many modern plant–insect associations. Herein, I present the results of specimen-based surveys of Campanian Age (83.6–72.1 Ma) macrofossil floras and their associated insect damage from the Kaiparowits Formation of Utah, USA, a fossiliferous deposit within the Western Interior. First, I describe a new genus of fossil laurel (Lauraceae), and analyze the plant–insect associations found on this taxon. After, I describe the diversity and intensity of plant–insect associations from the a single, well-sampled locality. I then describe a new fossil lyonetiid moth leaf mine, which represents the oldest fossil evidence of a cemiostomine leaf-mining moth, as well as the second oldest record of the Yponomeutoidea–Gracillarioidea clade. Then, I describe acarodomatia (mite houses) on fossil leaves, which constitute the oldest evidence for plant–mite mutualisms in the fossil record. Finally, to understand broad-scale and long-term patterns of insect damage in the fossil record, I analyze all available fossil plant–insect associational datasets spanning the Age of Angiosperms (ca. 76–2 Ma). These results indicate that insect preference for plant hosts may have changed through time as local plant diversity increased, but this may stem from differences in sampling regimes and difficulties in identification of fossil angiosperms. My findings collectively indicate that Late Cretaceous plant–insect associations are often novel, diverse, and may be evolutionarily tied to modern plant–insect associations, as well as the acquired insight into the limitations and future directions for this field of research.

PLANT–ARTHROPOD ASSOCIATIONS FROM THE WESTERN INTERIOR OF NORTH AMERICA DURING THE LATE CRETACEOUS

by

S. Augusta Maccracken

Dissertation submitted to the Faculty of the Graduate School of the
University of Maryland, College Park, in partial fulfillment
of the requirements for the degree of
Doctor of Philosophy
2020

Advisory Committee:
Professor Jeffrey Shultz, Co-chair
Curator Conrad C. Labandeira, Co-chair
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Professor Charles F. Delwiche
Curator Ian M. Miller

Dedication

For my mother, Karen.

Thank you for thirty-one years of unwavering love, support, and for fostering my connection with nature.

You are unrivaled in all the 3.48 billion years of life on Earth.

Foreword

With the approval of the dissertation co-directors, Dr. Jeffrey Shultz and Dr. Conrad Labandeira, the dissertation committee members, and the Department of Entomology Graduate Director, Chapter 2 of this dissertation is included as previously published research. The citation for the publication is as follows:

Maccracken, S. A., I. M. Miller, and C. C. Labandeira. 2019. Late Cretaceous domatia reveal the antiquity of plant–mite mutualisms in flowering plants. Biology Letters 15(11):20190657.

Under the guidelines of the graduate catalogue for the inclusion of one's own previously published materials in a dissertation, I affirm that I was responsible for the inception of this manuscript and the majority of the manuscript preparations. This manuscript was reformatted to meet all dissertation requirements set forth by the Graduate School. All other aspects of the previously published manuscript were preserved in the dissertation. A letter from the dissertation co-directors, committee members, and the Department Chair was sent to the Dean of the Graduate School certifying that the examining committee has approved the inclusion of the manuscript. A copy of this letter can be found in Appendix A.

Acknowledgements

First, I thank my co-advisers, Conrad Labandeira and Jeffrey Shultz. Conrad, you have changed the way I see the world. I am forever indebted to you for the many years of kindness, patience, and tutelage. I will always treasure our months of fieldwork in Saltillo, Mexico. Jeff, your guidance and advice gave me the confidence to navigate life as a professional scientist. I took your critiques to heart and was fortified by your hard-won complements and dark sense of humor. My co-advisors are very different people and very different scientists. I am beyond lucky have benefited from both pools of knowledge.

Thank you to the rest of my dissertation committee, Dan Gruner, Chuck Delwiche, and Ian Miller. The completion of this dissertation would not have been possible without their thoughtful guidance and encouragement. Not all graduate students are as fortunate as I am to have a committee that is as dedicated to their success as are Dan, Chuck, and Ian. Above all, I thank Ian Miller for his decade-long mentorship and friendship. As a naïve college student asking for an internship, I couldn't have imagined the expeditions and research projects we would undertake over the next decade. I look forward to a lifetime of scientific collaboration. Also, thanks to Robyn Rissman and Wilson Rissman-Miller for their hospitality during my many and often lengthy visits to Denver.

I also thank Charles Mitter, who served as my first advisor and who helped me grow as a scientist and writer. I tremendously enjoyed our bi-weekly meetings, which could range from the newest scientific discoveries, to the latest departmental news, and back again. Your edits of my early writings were panic inducing—as if

someone haphazardly splashed red paint on the paper. Thank you. You pushed me to find my voice.

I would also like to thank my collaborators, who are also lifetime friends: Sandra Schachat, Claudia Serrano-Brañas, Belinda Espinosa-Chávez, Joe Sertich, Kirk Johnson, Jay Cheon-Sohn, Vincent "Skip" Lyles, Anshuman Swain, Lisa Boucher, and Tyler Lyson. A huge thanks goes out to the faculty and staff of the Entomology Department, especially Leslie Pick, Josh Kiner, Amy Yaich, Pam Biery, Jamie Carrigan, Eileen Jewison, Greg Hess, Bill Katsereles, and Kelly Hamby. I also owe a great deal of gratitude to my undergraduate volunteers, Reuven Bank, Gabrielle Bates, Elijah Boswell, James Kavanaugh, Garrett Kelly, and Tarlan Vatan. I thank the DMNS Leaf Whackers as well as the DMNS and NMNH collections staff members over the years.

Thank you to my family members for a lifetime of encouragement, as well as my colleagues, peers, and friends for their ceaseless support. In alphabetical order, I thank Alex, Heidi, & Andrew Adatto, Rich Barclay, Kay Behrensmeyer, Peter Coffey, Caitlin Colleary, Crystal Cooke, Mike Donovan, Boyce Drummond, Becca Eckert, Andrew Garavito, Hannah Franklin Grisham, Ryan Gott, Gene Hunt, Sarah Jacobs, Advait Jukar, Jeff Kirn†, Karen Kirn, Kathryn Kirn, Mike Kirn, Weez Kirn, Hans Lemke, Emma Locatelli, Chris Maccracken, Joan Maccracken, Winnie Maccracken-Keshawerz, Emma Parenteau, Andrew Simpson, Karla Sosa, Chris Taylor, Elske Tielens, Nichole Tiernan, Becca Wilson, and Scott Wing.

Most importantly, and with all my love, I thank my fiancé Yama Keshawerz. I am most grateful to you, my best friend, my quarantine buddy. These past six and a

half years have been some of the best years of my life and I look forward to spending a lifetime with you.

Funding for my graduate studies and research included:

The University of Maryland Department of Entomology & Gahan Fellowship

The University of Maryland Graduate School

The BIG TEN Academic Alliance Smithsonian Predoctoral Fellowship

The Wiley Dissertation Completion Fellowship

The Smithsonian Institution Scholarly Studies Award

Explorer's Club Washington Chapter Student Awards

The Paleontological Society's Bearded Lady Student Research Grant

The Society for Sedimentary Geology Student Assistance Grant

Western Interior Paleontological Society John Jenkins Memorial Scholarship

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Chapter 1: Introduction and Summary of Dissertation Findings

The evolutionary history of plants and their insect adversaries is a story told by the scars on fossil leaves. Insect damage on a single leaf captures one moment in time when an insect fed upon a plant, but it also reflects the millions of years of evolution leading up to that moment. The effects of insect herbivory on terrestrial ecosystems through time has been immeasurable over the past 400 million years (Labandeira 2007, Labandeira et al. 2014), and only recently have scientists begun to understand major themes of the diversity and intensity of plant and insect associations in the fossil record.

Studies on deep time plant–insect associations have captured dramatic periods of Earth's history, starting with the alien floras of the Carboniferous Period (385–298.9 Ma (Ma; mega-annum)) and Permian Period (298.9–251.9 Ma) (e.g. Maccracken and Labandeira 2020, Schachat et al. 2015, Scott and Taylor 1983, Xu et al. 2018). Recent studies also have revealed the profound changes of ecosystems immediately before and after the Cretaceous–Paleogene (K/Pg) extinction event 66 million years ago (Ma) (ex. Donovan et al. 2018, Donovan et al. 2014, Labandeira et al. 2002b, Wilf et al. 2006) and during a brief period of intense global climate change, the Paleocene-Eocene Thermal Maximum at 55 Ma (Currano et al. 2010, Currano et al. 2008). However, there remains a wide gap in our knowledge about how insect herbivores responded to the rise and initial early radiation of flowering plants (angiosperms) throughout the Cretaceous Period.

Plants and insects of the Cretaceous Period (145–66 Ma) formed associations that are important precursors to those of today. During this period angiosperms overtook most ecosystems in a geologically brief period of time (Coiffard et al. 2012, Doyle et al. 1999, Heimhofer et al. 2005) and angiosperms now make up the majority of vascular plant life on earth today (Willis 2017). Despite being the inception of extant ecosystems we know today, the Cretaceous Period is one of the most poorly understood intervals of time for plant–insect associational studies (Figure 1.1). Plant–insect associations from the dawn of flowering plants to the terminal Cretaceous (~130–66 Ma) are a roadmap for the diversity of interactions we see in extant ecosystems and yet our understanding of Cretaceous plant–insect associations currently is insufficient. The research presented in this dissertation is among the first to step into the world of Cretaceous plant–insect associations and includes the first systematic study of plant–insect associations from the Campanian Age (83.6–72.1 Ma). To highlight the importance of this new research and because studies of deep time plant–insect associations broadly explore the two most diverse groups of terrestrial organisms, angiosperms and insects, this chapter includes a history of plants, insects, and their ecological associations. I also outline the geologic context, methodology, and summarize the findings for the research presented in this dissertation.

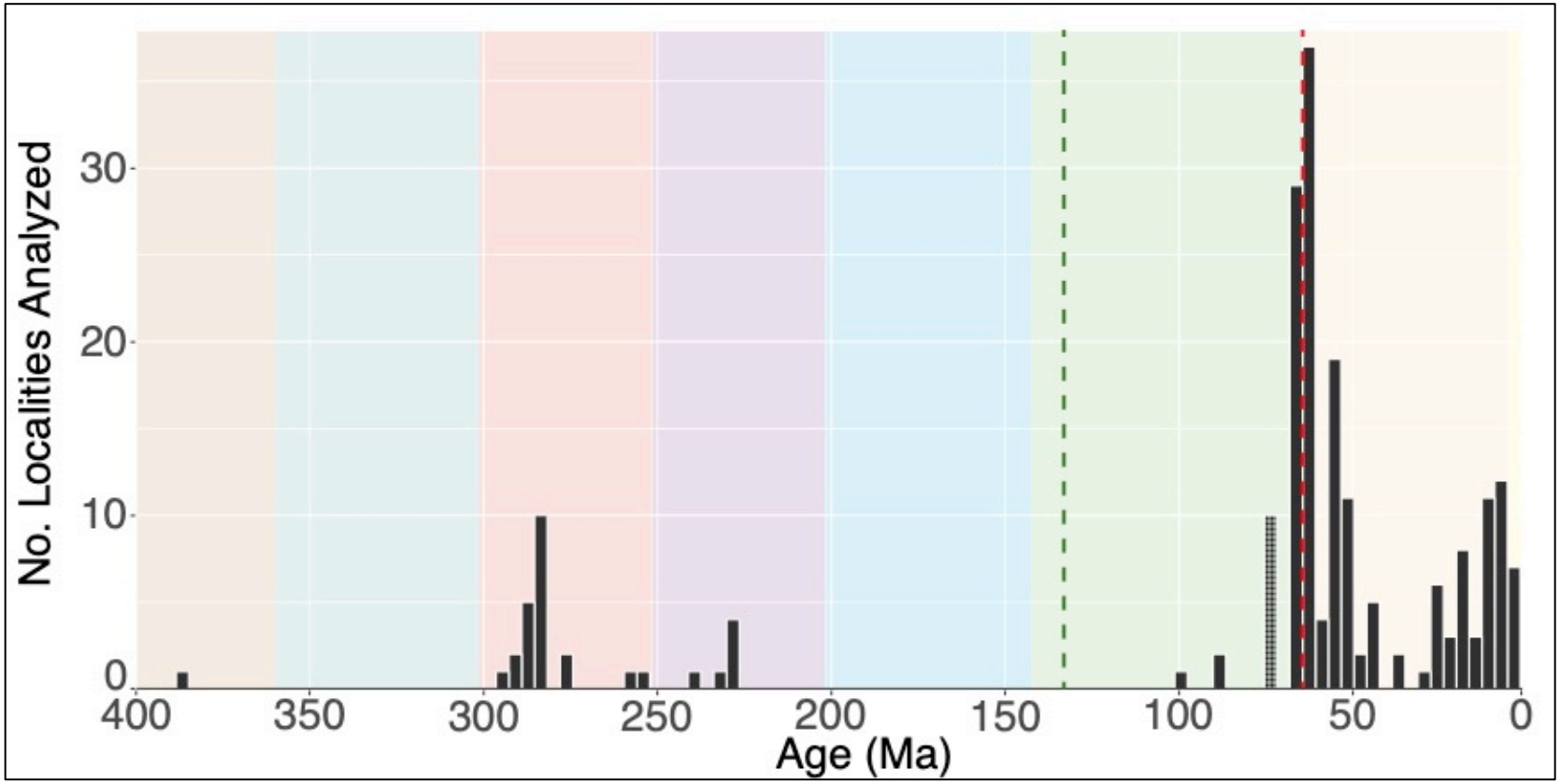


Figure 1.1: Localities analyzed for insect herbivory through time. Background color corresponds to Period, from the Devonian Period (here starting at 400 Ma) to the Quaternary Period (present). Localities included in this dissertation are denoted by the box-patterned bar (ca. 75 Ma). The green dashed line marks the first appearance of angiosperm fossils during the Early Cretaceous and the red dashed line marks the Cretaceous/Paleogene (K/Pg) extinction event. Only entire floras analyzed for herbivory were included in this analysis, although there are many more instances of herbivory described from specific plant hosts and assessments of specific damage types. Data for plot compiled by S. A. Maccracken using literature search.

Evolutionary Background

The Rise of Angiosperms

We live on an earth dominated by angiosperms. Today, flowering plants make up 96% of the terrestrial vegetation and there are an estimated 369,000 species (Pennisi 2009, Willis 2017). However, in the context of vascular plants, the world is only recently dominated by angiosperms. Knowledge of the history of vascular plants gives us a baseline to better understand the importance for the evolution of angiosperms. The earliest land plants were relatively simple spore-producing, non-vascular plants similar to extant bryophytes (mosses, liverworts, hornworts) (Delwiche and Cooper 2015); among the earliest spores known in the fossil record, tetrad spores from the late Ordovician (ca. 450 Ma) (Gray et al. 1982) and early Silurian (ca. 430 Ma) (Gray and Shear 1992, Taylor and Taylor 1993) provide strong evidence for the spore-producing phase of land plants (Willis and McElwain 2014). Non-vascular charophytes (freshwater green algae), bryophytes, and some extinct Devonian lineages were then preceded by vascular plants, such as lycophytes (fern allies), sphenopsids (horsetails), and ferns by ca. 430 Ma (Figure 1.2) (Willis and McElwain 2014). Seed plants evolved from the hornwort lineage around 380 Ma and greatly expanded during the Permian Period (299–252 Ma) (Willis and McElwain 2014), a time of great environmental change. It was not until the Mesozoic Era that the first angiosperms evolved (Crane et al. 1995, Herendeen et al. 2017, Hughes and McDougall 1994, Lupia et al. 1999), and even longer still until they became predominant on the landscape (Coiffard et al. 2012, Heimhofer et al. 2005, Wing et al. 1993). The rapid rise and ascendency of angiosperms is unrivaled in magnitude in

the evolutionary history of plants (Berendse and Scheffer 2009, Dilcher 2001) (Figure 1.3).

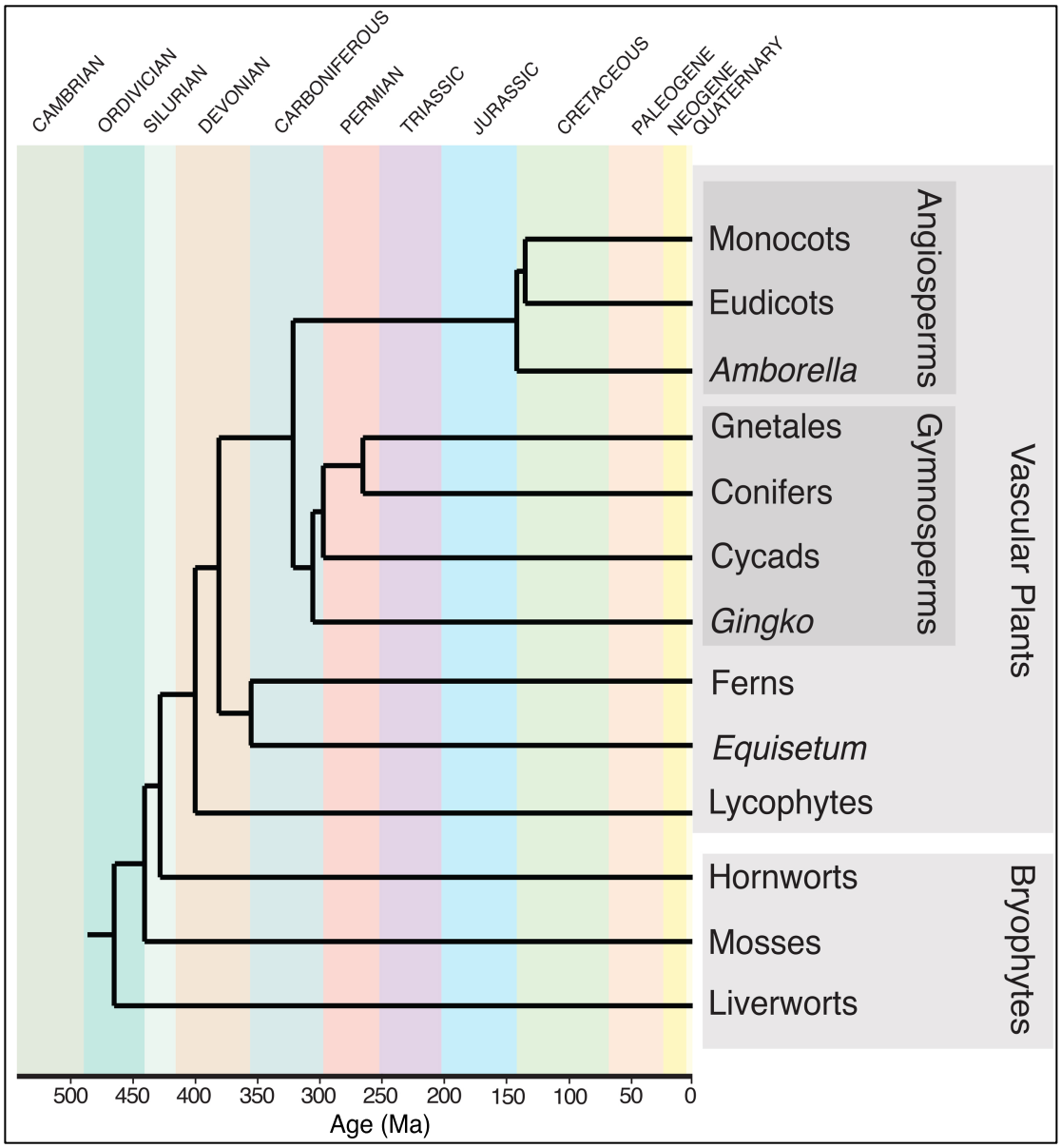


Figure 1.2: Phylogeny of land plants using a composite hypothesis of clade relationships. Figure created from hypothesized relationships between plant clades in Palmer et al. 2004, Sessa et al. 2014, and Stevens and Davis 2001.

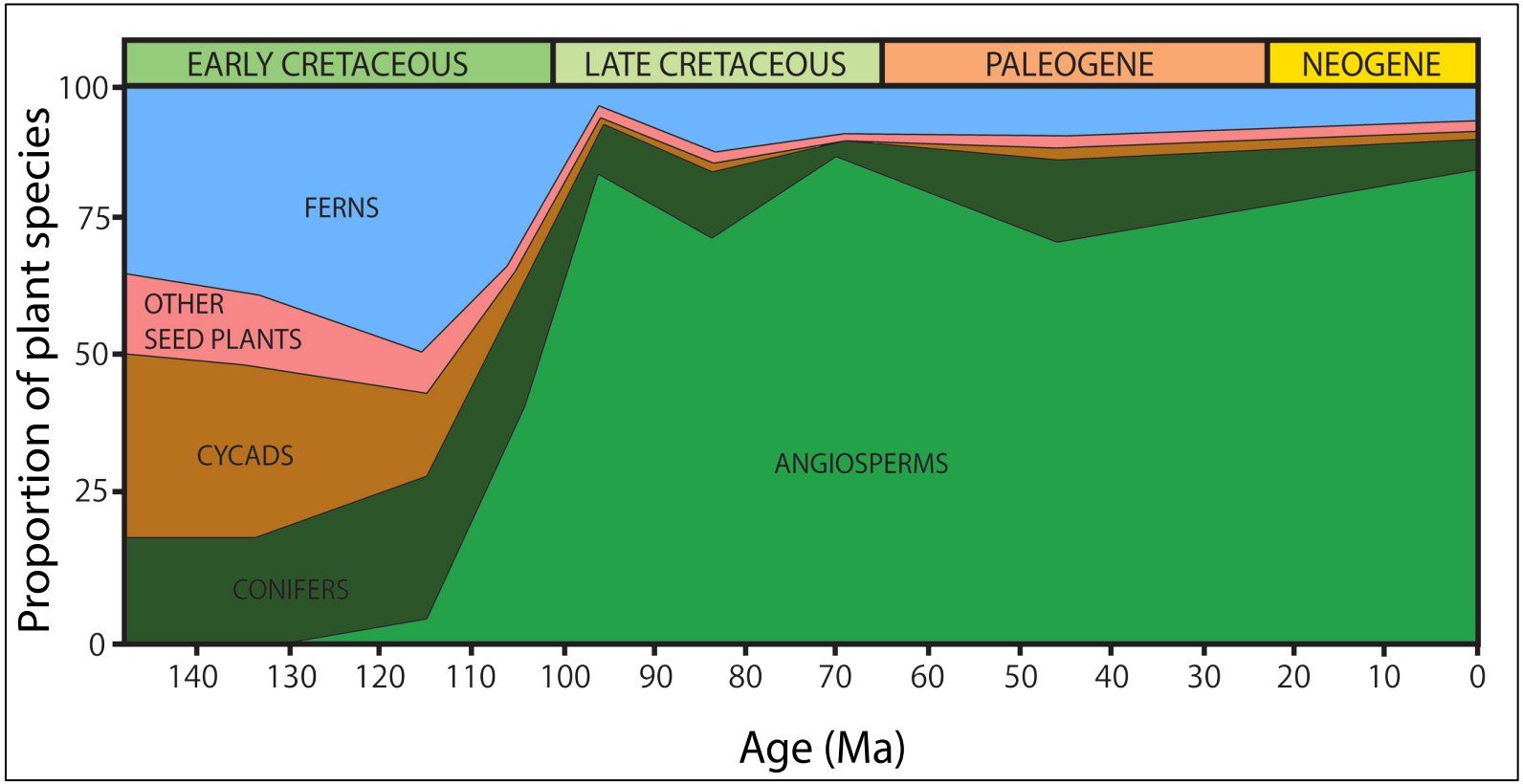


Figure 1.3: Seed plant and fern species through time. Note the rise and radiation of angiosperms in the Cretaceous Period. Figure redrawn from Crane 1987, Lidgard and Crane 1988, de Boer et al. 2012, Fagua et al. 2017, reproduced with permission from journal (license for content #4926051157679).

Darwin referred to the sudden appearance of angiosperms in fossil deposits as an “abominable mystery” (Darwin and Seward 1903). Despite 150 years of paleontological, ecological, and genetic discoveries, the rapid rise of angiosperms has many unanswered questions, including when they originated. The timing of angiosperm evolution is hotly, and on occasion, tactlessly debated (ex. Wang 2017). The oldest undisputed angiosperm fossils are pollen grains that date to the Early Cretaceous Period (ca. 136 Ma) (Crane et al. 1995, Herendeen et al. 2017, Hughes and McDougall 1994, Lupia et al. 1999). The earliest angiosperms likely predate their fossil record, common in many lineages, making fossil-calibrated molecular phylogenies important tools for dating this clade. Molecular phylogenies have placed the origin of angiosperms in the Cretaceous Period (139.35–136 Ma) (Magallón et al. 2015), the Jurassic Period (179–158 Ma) (Wikström et al. 2001), and even the Triassic Period (228–217 Ma) (Smith et al. 2010). Regardless of the uncertainty around the origination of flowering plants, of which Magallón et al. (2015) appear to have the most realistic calibration dates when compared to the fossil record, herbaceous angiosperm mesofossils and macrofossils are diverse and abundant by the Barremian–Aptian transition (late Early Cretaceous, ca. 125 Ma (Feild et al. 2011, Friis et al. 2011, Oakley and Falcon-Lang 2009, Philippe et al. 2008, Wheeler and Lehman 2009, Wheeler and Baas 1991). Throughout this time interval there are major ecological transitions as angiosperms diversify and outcompete older lineages of plants (Coiffard et al. 2012).

From the early to mid Mesozoic Era, gymnosperms and ferns dominated terrestrial ecosystems and filled most available plant niches until the rise of

angiosperms (Lidgard and Crane 1990). Coiffard et al. (2012) divided the rise and radiation of angiosperms into three phases. The first phase (136–125 Ma) consisted of relatively exclusive environments of gymnosperms and ferns, with rare aquatic angiosperms. Gymnosperms and ferns occupied all non-aquatic habitats and angiosperms became established in riparian corridors. During the second phase (112–100 Ma) angiosperms increased in species number and occupied a greater ecological breadth. In addition to aquatic and riparian niches, flowering plants began to colonize floodplains. During the third phase (100–94 Ma) angiosperms were widespread, speciose, and filled most ecological niches. Arborescent life-habits of angiosperms were also evolving, which further increased competition between angiosperms and gymnosperms attributable to overlapping niche space (Coiffard et al. 2012). By the Campanian Age (83.6–72.1 Ma), many of the major eudicotyledon clades had differentiated (Crane et al. 1995). It is in this relatively short time interval during the Cretaceous Period that we see the ascendancy of angiosperms; however, ecological interactions between angiosperms and insects during this time interval are poorly known and the fossil record of insects is likewise depauperate (Grimaldi and Engel 2005, Ross et al. 2000). The limited number of insect body fossil deposits and plant–insect research projects in this interval is problematic because the associations between insects and vascular plants, including herbivory and pollination, are hypothesized to play a major role in the diversification of both groups of organisms (ex. Bagchi et al. 2014, Bascompte and Jordano 2007, Cruaud et al. 2012, Ehrlich and Raven 1964, Janz 2011, McKenna et al. 2009, Wiens et al. 2015).

Insect Diversity and the Fossil Record

Insects (Phylum Arthropoda, Class Hexapoda) are the most speciose and abundant animals on Earth today, with recent predictions for total species diversity ranging between 5 and 20 million (Foottit and Adler 2009, Gaston 1991, Mora et al. 2011, Nielsen and Mound 2000, Stork 1988). Insects are found in every major terrestrial environment and the combined effect of insects on ecosystems through time is immense. The insect fossil record spans ca. 410 million years (Shear et al. 1984, Whalley and Jarzembowski, 1981) and it is hypothesized that insects first evolved at ca. 480 Ma (Misof et al. 2014) based on molecular data with fossil calibrations (Figure 1.4), with herbivorous insects evolving by ca. 410 Ma (Labandeira et al. 2014).

The insect fossil record can be considered both moderately complete at the family taxonomic level, but distressingly incomplete at the genus and species level when the fossil record is compared to hypothesized insect species diversity through time (Labandeira and Eble 2005, Labandeira and Sepkoski 1993). Although the body fossil record of insects capture all known orders of insects (32 modern orders, ca. 14 extinct orders) and over 1300 families, including approximately 70% of modern families (Labandeira 1994), the vast majority of ancient species have either not been discovered yet or are wholly unpreserved as fossils (Schachat and Labandeira in press). Furthermore, the record of insect fossil diversity is not evenly distributed through time and space, which can distort signals of diversity, such as the Signor–Lipps effect (Signor et al. 1982) and the Pull of the Recent effect (Raup 1979). At first glance, the Cretaceous insect fossil record may be considered well sampled due

to a small number of extensive amber deposits (Ding et al. 2003, Grimaldi and Engel 2005), yet in general, Cretaceous, especially the Late Cretaceous, insect fossils are remarkably sparse.

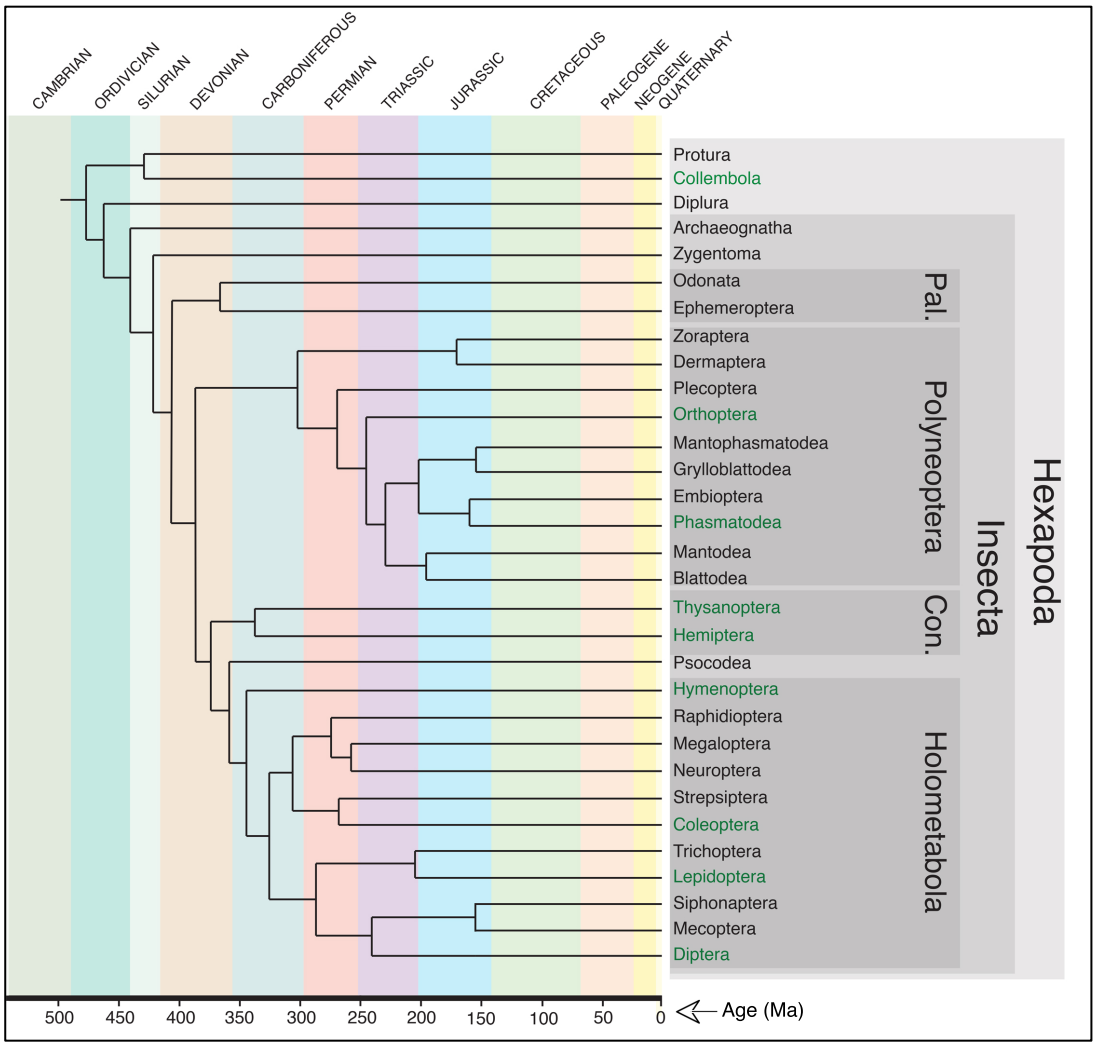


Figure 1.4: Generalized molecular phylogeny of extant insect orders through time. Nine of the 31 insect orders include herbivorous species (denoted by green text), including all four of the largest orders (Coleoptera, Diptera, Hymenoptera, and Lepidoptera). Figure adapted from hypothesized relationships presented in Misof et al. 2014), reproduced with permission from journal (license for content #4926050801134). Pal. Palaeoptera; Con. Condylognatha.

The best record of Cretaceous insects comes from the Burmese (Myanmar) amber, which dates to ca. 99 Ma and comprises 34 orders, 300 families, and 867

described species (Ross 2015, 2018). However, phytophagous insect fossils from the Western Interior of North America are relatively rare and mostly known from a small number of Late Cretaceous amber deposits (Hillaire-Marcel et al. 2008, McKellar and Wolfe 2010, Pike 1994, 1995). Despite the past 30 years of highly productive Cretaceous insect research (Grimaldi and Engel 2005), insect diversity curves for this time period remain contentious, especially in response to extinction and radiation events, such as how the radiation of angiosperms influenced insect diversity (and vice versa) throughout the Cretaceous Period (Jarzembowski and Ross 1996, Labandeira and Sepkoski 1993, Ross et al. 2000, Schachat et al. 2019).

Labandeira and Sepkoski (1993) found that the taxonomic family-level diversity of insects was nearly static throughout the Early and Late Cretaceous, notably during the rise of angiosperms. This was an unexpected and highly contentious result within the paleoentomology community, as it was assumed that insect diversity would increase in-step with flowering plants. These findings were interpreted as being at odds with longstanding 'coevolutionary arms race' theories, in which herbivorous insects and angiosperms fueled successive species radiations in one another (Ehrlich and Raven 1964, Farrell 1998, Janz 2011, McKenna et al. 2009, Mitter et al. 1988, Moreau et al. 2006). Subsequently, there have been several independent re-analyses of family level diversity during this interval (Jarzembowski and Ross 1996), most notably Schachat et al. (2019), which used mark-recapture methodology and found a steady increase in family-level diversity in the Early Cretaceous and a steep increase in diversity during the Albian. This increase, however, started before and during the early evolution of angiosperms, when they

were not especially diverse or abundant (Schachat et al. 2019).

Why didn't the number of insect families change during the Cretaceous in relation to the diversification of angiosperms? First, the relative stasis of family-level diversity for herbivorous insects may reflect the evolutionary timing of insect lineages; many families of insects originated throughout the late Paleozoic and early Mesozoic Eras (see Misof et al. 2014) and in association with spore-bearing and seed-producing plant hosts (Labandeira 2002b, 2005, Rasnitsyn 1988). Parasitoid insects, a large component of modern insect diversity, also diversified throughout the Jurassic Period and underwent a radiation during the Aptian–Albian interval prior to the ecological dominance of angiosperms (Labandeira 2002b, 2005, Rasnitsyn 1988, Schachat et al. 2019). Labandeira and Sepkoski (1993) postulated that diversification of insects during the rise of angiosperms might have occurred at subfamilial taxonomic ranks. Origination and extinction rates may have also impacted the diversity curve for Cretaceous insect families; if extinction and origination rates are equal, including if both spike dramatically, there would be stasis in the number of insect families (Labandeira 2005, Labandeira 2014, Schachat and Labandeira in press). As conifers, cycads, other now-extinct gymnosperm lineages, and to a lesser extent ferns (Schneider et al. 2004) were replaced by new species of angiosperms (Coiffard et al. 2012, Lidgard and Crane 1990, Lupia et al. 1999), it is likely that some herbivorous insects lost their host plants and went extinct, while other herbivorous and pollinating insects became more speciose (Fagua et al. 2017, McKenna et al. 2009, McKenna et al. 2015, Ross and Jarzembowski 1993, Ross et al. 2000, Zhang and Wang 2017). Finally, changes in insect plant host preference may

have also spurred the coevolution between angiosperms and herbivorous insects without an increase in family-level diversity (Labandeira 2014). The host plant preferences of phytophagous insect families from the Jurassic Period to the Paleogene Period generally shift from gymnosperms to angiosperms, coupled with the extinctions and originations of other insect clades (Labandeira 2014) (Figure 1.5). Continuing research into insect diversity before and throughout the rise of angiosperms will undoubtedly shed light on this event. Complementary lines of evidence into how herbivory changed during this time period, such as the record of insect damage on fossil leaves, can provide independent evidence of insects when the body fossil record is sparse and, moreover, provide novel information on the ecologies of ancient insects and their associations with plants (Labandeira 1998b).

The Fossil Record of Plant–Insect Associations

Fossil plant material, including insect damaged leaves, is the basis for reconstructing the diversity of ancient terrestrial landscapes and their ecological interactions. The fossil record of plant–arthropod associations is comprised of mimicry (Wang et al. 2012), mutualisms (Maccracken et al. 2019, O'Dowd et al. 1991), notably insect pollination (Labandeira 2010, Labandeira et al. 2007b, Peris et al. 2017, Wappler et al. 2015b), and insect herbivory, which is among the most dynamic and copious of these associations (see Pinheiro et al. 2016). Evidence for the damage that herbivorous insects inflict—the punctures, skeletonization, galls and leaf mines in fossil leaves—constitute one of the richest ecological sources of evidence available on species interactions of any kind from the distant past. Many studies on deep time insect herbivory have focused on epochal floras or single plant–insect

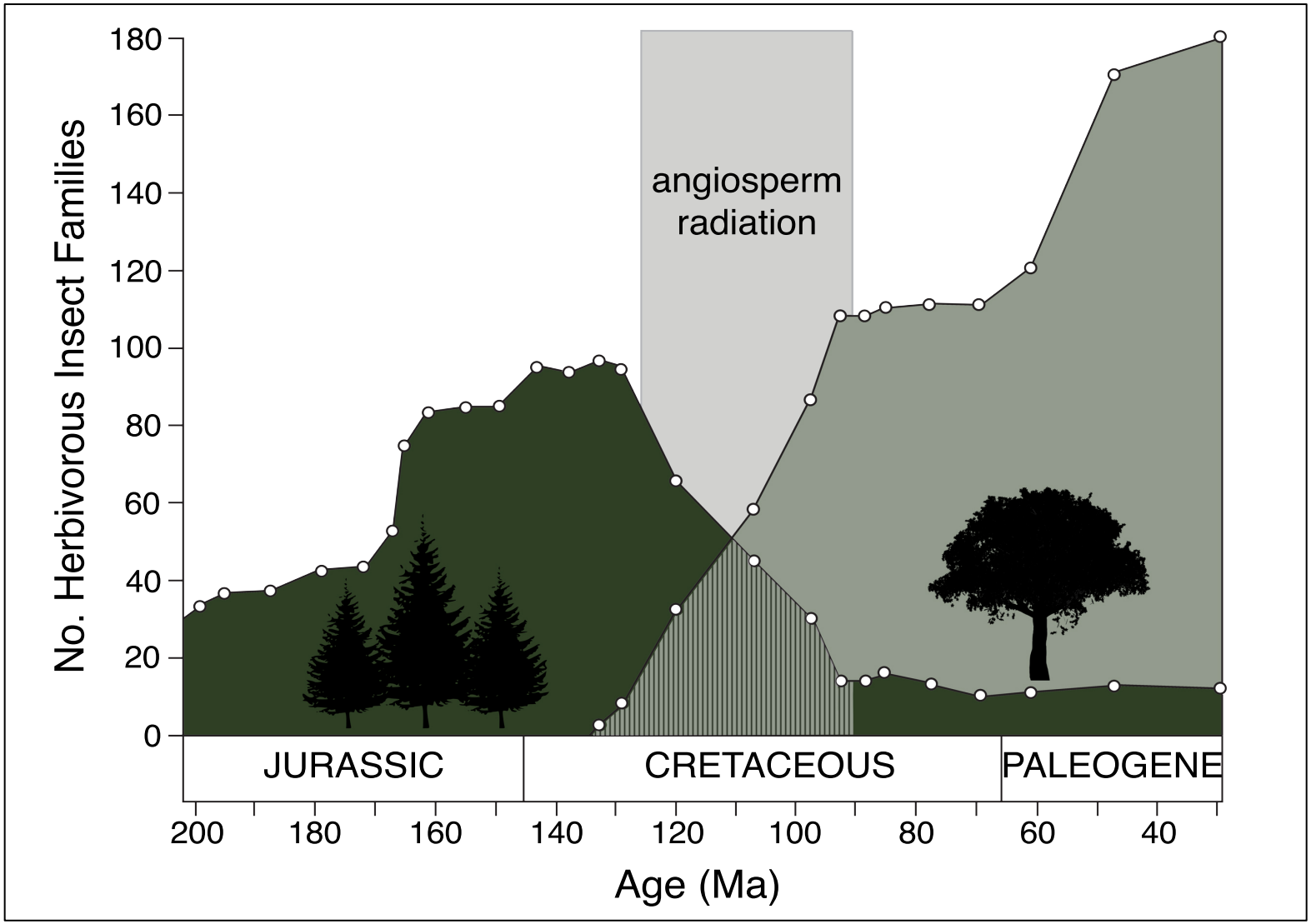


Figure 1.5: Insect family diversity and host plant preference changes throughout the late Jurassic Period to the Paleocene Period. Dark green is gymnosperm-feeding and light green is angiosperm-feeding families. Modified from Labandeira (2014). Reproduced with permission from journal (license for content #4926060730978).

associations. Collectively, the temporal and spatial patterns of deep time plant–insect associations provide fundamental information on ancient food-web structure (Dunne et al. 2014, Feng et al. 2017, Prevec et al. 2009, Wilf 2008), changes in climate (Currano 2009, Currano et al. 2010, Currano et al. 2008, Winkler et al. 2009a), the evolution of insect feeding guilds and specific insect clades (Labandeira 2006b, Sarzetti et al. 2008, Sohn et al. 2019a), host plant specialization (Jud and Sohn 2016, Wilf et al. 2000, Winkler et al. 2009a), and extinction events (Donovan et al. 2016, Donovan et al. 2018, Donovan et al. 2014, Labandeira et al. 2002b, Wappler et al. 2009, Wilf 2008, Wilf et al. 2006).

Among the first instances of fossil insect herbivory reported in the scientific literature were descriptions of galls on fossil leaves from the Oligocene Period (Scudder 1886), Cretaceous galls (Lesquereux 1892), and now dubious leaf mines on Permian ferns (Potonié 1893). Other early descriptions of insect damage includes galls from the Oligocene Period (Brues 1910) and Pleistocene Period (Berry 1909); Eocene galls on figs (Cockerell 1910); and various fossil plant–insect associations described during the mid-twentieth century (ex. Brooks 1955, Chaney 1920, Hoffman 1932) and in wood (Brues 1936). Systematic descriptions of insect damage on fossil leaves began in the mid-1970s through the 1990s (ex. Crane and Jarzembowski 1980, Hickey and Hodges 1975, Liebhold et al. 1982, Opler 1973, 1982, Rozefelds and Sobbe 1987, Scott et al. 1985, Scott and Paterson 1984, Scott and Taylor 1983) and since the 1990s, the insect damage research has become more widespread, systematic, and formalized, most notably with the advent of the *Guide to Insect (and Other) Damage Types on Compressed Fossil Plants* (Labandeira et al. 2007c).

The renaissance of fossil insect herbivory studies occurred during the 1990s, when paleobiologists began systematically analyzing and quantifying insect damage across periods of time and for entire floras (Beck and Labandeira 1998, Labandeira 1998a, b, Labandeira et al. 1994, Labandeira et al. 1995, Wilf and Labandeira 1999). The seminal paper for implementing the functional feeding group–damage type system of plant–insect analysis was Wilf and Labandeira (1999). During the 2000s and 2010s insect herbivory studies expanded into previously unstudied geographic regions and time periods (ex. Adroit et al. 2018a, Adroit et al. 2018b, Adroit et al. 2016, Currano 2009, Currano et al. 2010, Currano et al. 2008, Khan et al. 2014, Knor et al. 2012, Labandeira et al. 2016, Möller et al. 2017, Müller et al. 2015, Pinheiro et al. 2012, Prokop et al. 2010, Su et al. 2015, Wappler et al. 2009, Wappler and Grímsson 2016, Wappler et al. 2012). Recent neontological studies have ground-truthed observations from the fossil record (Adams et al. 2010, Carvalho et al. 2014, Sohn et al. 2019b) and paleontological studies have also undertaken new statistical analyses and sampling regimes, which are more closely aligned with techniques of neontologists (Currano 2009, Currano et al. 2010, Currano et al. 2019, Gunkel and Wappler 2015, Maccracken and Labandeira 2020, Schachat et al. 2015, Schachat et al. 2014, Schachat et al. 2018, Schachat et al. 2020). In general, the study of deep time plant–insect associations has become more sophisticated, detailed, and rigorous through time, as well as more finely partitioning the types of insect damage seen on fossil plant specimens. Finally, a formative study by Pinheiro et al. (2016) recently analyzed a large dataset (>70,000 specimens) of plant–insect associational studies for the past 385 million years and found that damage type diversity generally increased

with geologic age and temperature (Pinheiro et al. 2016).

The earliest unequivocal arthropod herbivory, geologically speaking, consists of sporangial and stem consumption from the earliest Devonian Period (ca. 410 Ma) of Europe (Kevan, Chaloner, and Savile, 1975, Labandeira 2007, Labandeira et al. 2014). Very limited herbivory has been documented for the Mississippian Epoch between 359–323 Ma (Iannuzzi and Labandeira, 2008). By the Carboniferous Period, between 327–309 Ma, arthropods herbivorized roots, leaves, seeds, and wood, and all major herbivorous arthropod feeding guilds had evolved (Labandeira 1998a, 2001, Scott and Taylor 1983), except for leaf mining, which first appears in the earliest Triassic of Russia (Krassilov and Karasev, 2008) and the Late Triassic Period of South African deposits (Labandeira and Anderson 2005). By the Early Cretaceous Period, the damage types created by insect herbivores appear essentially modern (Labandeira 1998c); hole feeding, margin feeding, skeletonization, surface feeding, piercing-and-sucking phloem and xylem sap feeding, leaf mining, galling, wood boring, and seed predation are extensive and well known before the advent of angiosperms (see Labandeira et al. 2007c and recent addenda for a record of Paleozoic and Mesozoic damage types). However, the Mesozoic Era in general and Cretaceous Period in particular is the poorest-sampled period of time for plant–insect associational studies (Pinheiro et al. 2016), and we expect to see both novel types of insect damage that would extend the record of many Cenozoic damage types into the early rise of angiosperms.

The majority of described Mesozoic plant–insect associations are isolated Triassic, Jurassic, and Cretaceous damage types, often single occurrences, on

particular plant hosts (Cenci and Adami-Rodrigues 2017, Estévez-Gallardo et al. 2019, Jud and Sohn 2016, Khan et al. 2014, Krassilov 2007, Krassilov and Shuklina 2008, Krassilov 2008a, Krassilov 2008b, Labandeira 1998c, Labandeira et al. 1994, Moisan et al. 2012, Vasilenko 2008, Wilf et al. 2000). There are a total of five descriptions of insect herbivory for entire floras in the early to mid-Mesozoic Era from ca. 250–90 Ma (Arens and Gleason 2016, Krassilov and Shuklina 2008, Labandeira et al. 2016, Scott et al. 2004, Wappler et al. 2015a), of which only two are mid-Cretaceous in age and include floras with angiosperms present (Arens and Gleason 2016, Krassilov and Shuklina 2008). Six studies analyze plant–insect associations at the terminal Cretaceous, with the goal of tracing insect herbivory across the K/Pg boundary and into the early Paleogene (Donovan et al. 2016, Donovan et al. 2018, Donovan et al. 2014, Labandeira et al. 2002a, Labandeira et al. 2002b), and several additional studies examine the recovery of plant–insect associations during the early Cenozoic (Donovan et al. 2014, Wappler et al. 2009, Wilf et al. 2006).

For comparison to the Campanian Age floras described in this dissertation, the studies of terminal Cretaceous plant–insect associations provide an important baseline, since they are 1) within 10 million years of one another, 2) use the same insect damage classification system, and 3) include large sample sizes across numerous localities. For example, a total of 9,292 fossil plant specimens were examined from the terminal Cretaceous Hell Creek Formation in the Williston Basin and the diversity of damage types was found to be moderate (North Dakota USA) (Labandeira et al. 2002a, Labandeira et al. 2002b). The diversity of plant–insect

associations from the latest Cretaceous (Maastrichtian) Lefipán Formation in Argentina was significantly greater than that of the Hell Creek, when data were standardized (Donovan et al. 2016, Donovan et al. 2018). Based on these Maastrichtian studies, the Campanian Age localities analyzed in this dissertation are expected to have a moderate- to high-diversity of damage types, made by insect herbivores that range from monophagous (fed upon a single plant host species) to polyphagous (fed upon many, unrelated plant host species).

Geologic Background

The research in this dissertation is focused on the Late Cretaceous of North America. By the Campanian Age (83.6–72.1 Ma), the Cretaceous Western Interior Seaway divided North America into several landmasses, with Laramidia to the west and Appalachia to the east (Hancock and Kauffman 1979) (Figure 1.6). Laramidia was an elongate, north-to-south oriented landmass that stretched from present day north-central México to northern Alaska and covered approximately 4 million km^2 (Sampson et al. 2010a). A north-south-trending mountain chain, the Sevier Orogeny, formed the backbone of this ancient landmass in the mid-latitudes of present-day California and Oregon. Rapid uplift and erosion, combined with foreland subsidence, preserved alluvial and fluvial plains (Roberts et al. 2013). These depositional settings entail flat, gently sloping depositional landforms created by rivers that carried sediment from the mountainous region eastward to the Laramidian coastline (Roberts et al. 2013). The broad alluvial/fluvial plain blanketing the shoreline is preserved as a number of fossil-bearing geologic formations, including the principal formation

examined for this dissertation.

The Kaiparowits Formation

The Kaiparowits Formation is located on the Kaiparowits Plateau in the Grand Staircase-Escalate National Monument in southern Utah, USA (paleolatitude 46.2^{o}N (Miller et al. 2013)) (Figure 1.6). Almon H. Thompson, a member of the Powell

Figure 1.6: Map of North America during the late Campanian (ca. 75 Ma). Kaiparowits Formation is noted by the yellow dot. Map used with permission from Colorado Plateau Geosystems (Blakey 2011).

Survey in the 1870s, popularized the name "Kaiparowits" (Blake 2017), although the area was inhabited by indigenous peoples for over 10,000 years (Spurr et al. 2004) and this was not among the earliest names for this region. Kaiparowits is a Paiute Indian word that translates to "Home of our People" (Blake 2017). It is a 1005-meter-thick package of sandstones, siltstones, mudstones, and conglomerates (Table 1.1) (Beveridge et al. 2020, Roberts et al. 2013). $^{40}Ar/^{39}Ar$ dating from throughout the formation indicate that it was deposited between 76.49 ± 0.14 and 74.69 ± 0.18 Ma, and is divided into one formal member and three informal members: the newly described and uppermost Upper Valley Member, and the informal upper, middle, and lower members, of which the middle member is richest in fossils (Beveridge et al. 2020, Roberts et al. 2013). The Kaiparowits Formation was formed from coastal plain deposits, occurring in a subtropical and relatively wet climate (mean annual temperature ca. 20°C and mean annual precipitation ca. 1.8 m) (Miller et al. 2013).

Table 1.1: Six facies associations and paleoenvironmental interpretations of the Kaiparowits Formation, as described by Roberts et al. (2013).

Facies Associations.	**Paleoenvironment.**	**Description.**
Intraformational conglomerates	High energy flow environments in river channels	May be thalweg deposits, sometimes sandy mudstones
Major tabular and lenticular sandstones	Meandering or anastomosing river channels	Bankfull widths 20-80m; bankfull depth 3-10m; often with adjacent crevasse splays
Minor tabular and lenticular sandstones	Crevasse splay and crevasse channel deposits	Plant material abundant
Finely laminated calcareous siltstone	Large shallow lakes	Plant material abundant, especially aquatic fern taxa
Inclined heterolithic sandstone and mudstone	Point bar lateral accretion in a tidally influenced channel	Rare in the Kaiparowits Fm.; DMNS Loc. 3642
Sandy mudstone and carbonaceous mudstone	Range of overbank deposits: perennial ponds & lakes, oxbow lakes, marshes, swamps, and large, slow moving channels	Suggestive of ever wet, low lying alluvial system with large, slow moving channels and well vegetated overbank sequences. Plant material abundant

These sediments are estimated to have been deposited between 10 to 100 km from the paleocoastline (Roberts et al. 2013). Abundant large and small river channels, ponds, lakes, and swamps dominated the landscape and preserved a wealth of organisms and trace fossils in this formation (Roberts et al. 2013).

The Kaiparowits is well-known for its exceptional diversity of organisms, including non-avian dinosaurs (Carr et al. 2011, Decourten and Russell 1985, Gates and Sampson 2007, Lund et al. 2016, Sampson et al. 2010b, Sampson et al. 2013, Zanno et al. 2013), birds (Farke and Patel 2012), pterosaurs (Farke and Wilridge 2013), squamates (Lively 2016, Lyson et al. 2017, Nydam 2013), amphibians (Gardner and DeMar 2013, Roček et al. 2013), crocodyliforms (Farke et al. 2014, Irmis et al. 2013), mammals (Cifelli 1990a, b, Eaton and Cifelli 1988, Eaton et al. 1999), fish (Brinkman et al. 2013, Kirkland et al. 2013), aquatic invertebrates (Roberts et al. 2008, Tapanila and Roberts 2013), and plants (Maccracken et al. in review-a, Miller et al. 2013). Insect body fossils from this formation are virtually absent, despite the high probability that insects were abundant and diverse (Labandeira 2006a, Labandeira and Eble 2005).

Kaiparowits Formation specimens are housed at the Denver Museum of Nature and Science in Denver, Colorado. The Kaiparowits Flora was collected by Dr. Ian Miller and colleagues from 2008–2020.

Research Objectives

Plant–insect associations from the Late Cretaceous of western North American ecosystems are poorly known and the research in this dissertation aims to identify and quantify Campanian plant–insect associations from the Kaiparowits Formation. Across the next five chapters, the overarching objectives are as follows:

1. Document the diversity of insect damage on fossil leaves from the Campanian Age flora from the Kaiparowits Formation (**Chapters 2, 3**)

2. Taxonomically describe new plant host species, novel arthropod damage types, and important plant–arthropod associations. (**Chapters 2–5**)

3. Analyze all available and suitable datasets of plant–insect associations during the age of angiosperms (ca. 140 Ma – present) for large-scale patterns of insect preference of plant hosts. (**Chapter 6**)

Brief Methodology

The first step in the analysis of plant–insect associations is to identify all plant hosts in the flora. Due to the high numbers of fossil leaf species at many localities, identification and description of Linnaean leaf taxonomy for each possible species was not feasible. Instead, leaves were categorized (i.e., binned) into macrofossil

morphotypes following the system devised by Johnson (1989) and elaborated by the Leaf Architecture Working Group (1999) (Figure 1.7). Binning allows the use of morphological characters to demarcate discrete taxonomic units before a morphotype is formally applied and described. Leaf venation, leaf margin features, leaf base and overall leaf shape are among the key features for morphotyping foliage within a flora. The Kaiparowits Flora was morphotyped by SA Maccracken and IM Miller. In some instances, taxonomic descriptions of plant hosts are necessary. All taxonomic descriptions follow the guidelines of the *International Code of Nomenclature for Algae, Fungi, and Plants (Shenzhen Code)* (Turland et al. 2018). Morphological descriptions of dicotyledonous angiosperms follow the terminology of the *Manual of Leaf Architecture* (Ellis et al. 2009).

The following criteria were used to distinguish herbivore-induced insect damage from physical damage, such as tearing, detritivory, or taphonomic processes. The first criterion is the presence of reaction tissue, in which cells are enlarged or multiplied along the site of damage (Brues 1924, Johnson and Lyon 1991, MacKerron 1976, Vincent et al. 1990). A second criterion is the targeting of a specific host-plant taxon or a particular plant organ that can be attributed to insect-specific patterns of damage, such as linear rows of punctures on or along primary veins, or small cusps occurring on the cut edge of a plant tissue (Gangwere 2017, Kazakova 1985, Keen 1952). A third criterion is the repetition of a damage pattern based on shape, size, and position of the damage on the plant (Bodnaryk 1992, Heron 2003). After herbivore damage was identified, it was classified by feeding guild, or functional feeding group, and damage type (Labandeira et al. 2007c).

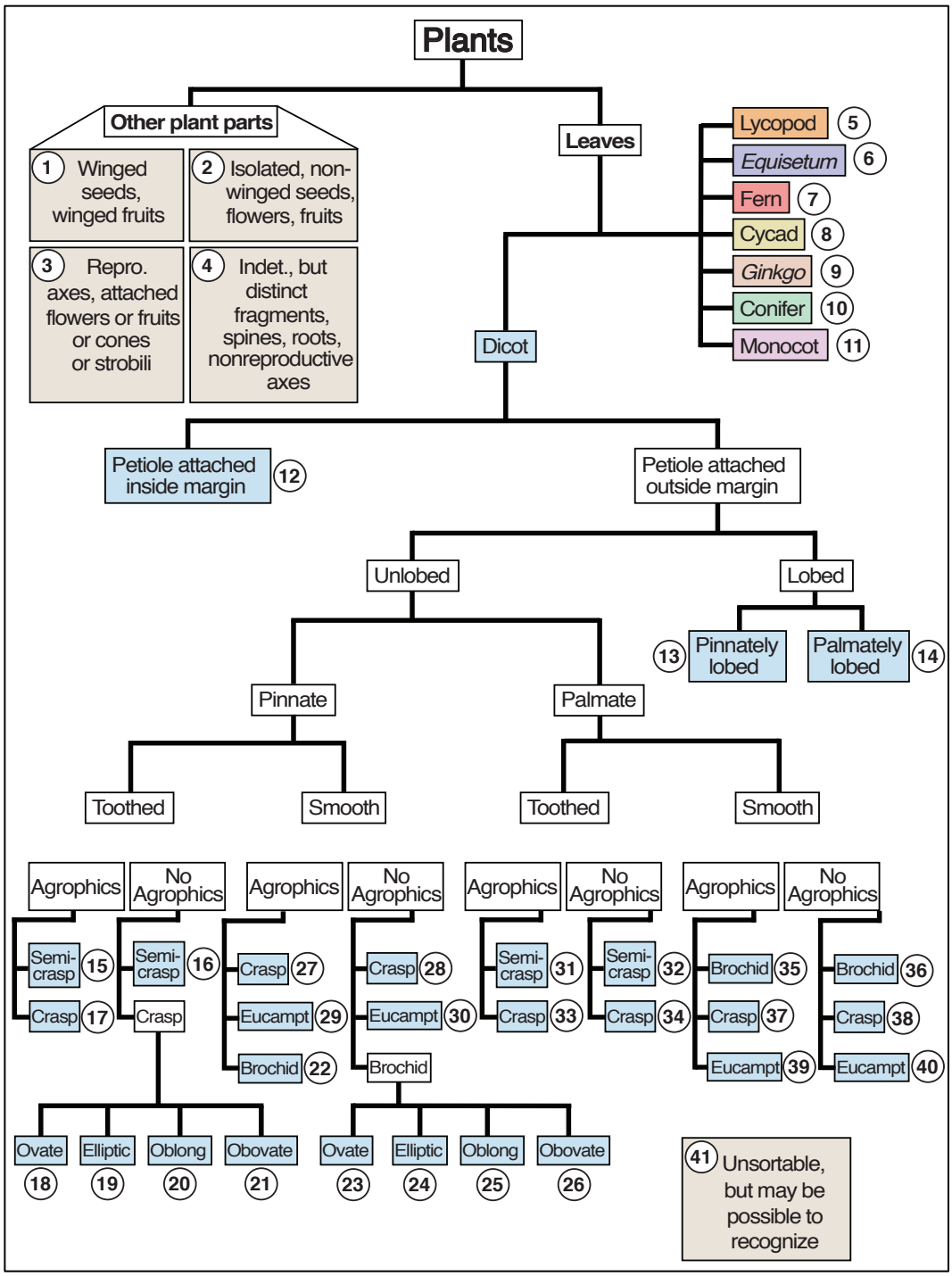


Figure 1.7: Flow chart showing a morphological binning of leaf macrofossils to assist in the morphotyping process devised by Johnson (1989) and elaborated by the Leaf Architecture Working Group (1999). The "bin" system in this flow chart is not formally published. It is in use by the working group at the Denver Museum of Nature & Science and redrawn here with permission (pers. comm. I.M. Miller). Please inquire with the Denver Museum of Nature & Science Department of Earth Sciences for reproduction permission. Brochid = brochidodromous, Crasp = craspidodromous, Eucampt = eucaptodromous.

The classification of each instance of herbivore damage followed the system of Labandeira et al. (2007c), including recent addenda to the *Guide to Insect (and other) Damage Types on Compressed Plant Fossils*. The damage was initially categorized into one of several functional feeding groups: 1) hole feeding; 2) margin feeding; 3) surface feeding; 4) skeletonization; 5) piercing and sucking; 6) oviposition; 7) galling; and 8) leaf mining. Discrete, diagnosable damage types were documented within each functional feeding group and assigned a damage type number. Damage types are defined by the distinctive shape, size, extent, and location of herbivore damage on the affected leaf, as well as being rated for host specificity: 1 or generalized (polyphagous), 2 or intermediate (oligophagous), and 3 or specialized (monophagous) (Labandeira et al. 2007c). The convergence of herbivore mouthparts and feeding behaviors make genus or species level identifications of the insect culprit rare, although some margin feeding, leaf mines, galls, and scale-insect feeding marks can be traced to extant lineages (ex. Jud and Sohn 2016, Sarzetti et al. 2008, Wappler and Ben-Dov 2008, Wilf et al. 2000, Winkler et al. 2010). Pathogen damage was not documented because of the difficulty of recognition, although the next version of the *Guide to Insect (and other) Damage Types on Compressed Fossils* will provide keys and other diagnostic criteria for recognition.

Plant–insect associational data includes both qualitative and quantitative data. The qualitative data, outlined above, consist of functional feeding groups, damage types, and host plant specificities. The qualitative data determine if the insect feeding guilds on a particular host-plant taxon, the diversity of damage types, host specificities, and occasionally identities of the phytophagous insect responsible for

the damage. Quantitative data collection consists of the proportion of damaged leaves, the richness of damage types, and the percent of surface area herbivorized by insects (herbivory index).

Summary of Dissertation Findings

Documentation and analyses of plant–insect associations from the Late Cretaceous Kaiparowits Formation provides the first evidence of the diversity and ecology of herbivorous insects from this formation. These findings are not only important for future reconstructions of the Kaiparowits ecosystems, but also document the earliest occurrence of a lineage of lepidopteran leaf miners and of plant–mite mutualisms in the fossil record. Please note that each chapter is prepared for publication in a specific peer-reviewed journal and some repetition occurs among chapters, as well as differences in style, spelling (American versus British English), and supplementary materials, based on the prospective journal's requirements.

In Chapter 2, "Insect herbivory on *Catula gettyi* gen. et sp. nov. (Lauraceae) from the Kaiparowits Formation (Late Cretaceous, Utah, USA)", I present the first formal description of a plant taxon from the Kaiparowits Formation and survey the insect herbivory found on the leaves of this new species. With over 1,500 specimens from a single locality, *Catula gettyi* is one of the best-sampled fossil plant taxa from the Late Cretaceous, and there is a total of 40 patterns of insect damage found on these specimens. This relatively high diversity of damage types also provides

evidence for a number of different types of insect herbivores, including those with chewing mouthparts (i.e. beetles, grasshoppers, caterpillars, etc.), insects that puncture the leaf surface with stylet-like mouthparts (i.e. hemipterans, thrips, etc.), insects adapted for leaf mining, and galling insects.

Chapter 3, "Plant–insect associations from the Campanian (Late Cretaceous) of Utah, USA", also includes quantitative analyses of plant–insect associations from the Kaiparowits, which encompasses all plant host specimens from the JARS locality (DMNH loc. 3725). The diversity of plant hosts at JARS include angiosperms, as well as a small number of lycopsids, pteridophytes, sphenophytes, gymnosperms, and unassociated reproductive plant organs. The results of this study include a moderate diversity of insect damage when compared to that of *Catula gettyi*, the targeting of several plant hosts by particular clades of insect herbivores, as well as a possible intercontinental distributional range of oviposition on the floating aquatic angiosperm *Quereuxia* spp.

Chapter 4, "A new Late Cretaceous leaf mine *Leucopteropsis spiralis* gen. et sp. nov. (Lepidoptera: Lyonetiidae) and the deep time origin of a common agricultural pest", describes a new fossil leaf mine from the Kaiparowits Formation, which is the earliest record of a lyonetiid leaf-mining moth, as well as the second oldest record of the Yponomeutoidea–Gracillarioidea clade. This discovery provides an important Late Cretaceous (~76 Ma) calibration point within the lepidopteran phylogeny and is an indicator for the antiquity of the most diverse lepidopteran group, Ditrysia. It also underscores the importance of ichnofossils in the lepidopteran fossil record, since body fossils of butterflies and moths are rare (Sohn et al. 2014).

The discovery of acarodomatia (mite houses) in fossil leaves from the Kaiparowits Formation in Chapter 5, "Late Cretaceous Domatia Reveals the Antiquity of Plant–Mite Mutualisms in Flowering Plants", documents the oldest known acarodomatia in the fossil record (ca. 75.5 Ma). This fossil acarodomatia extends the record of fossil domatia by over 25 million years and I describe the evolutionary timing of suitable host plants and the first acarodomatia. Acarodomatia are found almost exclusively on woody angiosperm species, and woody angiosperms are not common until ~100 Ma. Consequently, acarodomatia likely first evolved in conjunction with early woody dicot angiosperms, which first appeared approximately 25 million years preceding the newly discovered Campanian acarodomatia.

Finally, in Chapter 6 "Widespread biases in deep time plant–insect associational studies obscure potential patterns of insect preferences throughout the Age of Angiosperms", I analyzed all available datasets of plant–insect associations from the Cretaceous Period to the Quaternary Period to understand how insect herbivory has changed though time. Although insect preference for plant hosts significantly changed through time and as plant diversity increased within an ecological community, these results illuminate how sampling regimes and the difficulties of taxonomic identification for older fossil plants prevents us from understanding the causal mechanisms that drive insect herbivory over long periods of geologic time.

In total, the discoveries and analyses presented in this dissertation allow us to better reconstruct the ancient ecosystems of the Kaiparowits Formation, recognize

some of the first plant–insect associations from a Campanian Age deposit, and trace the evolutionary trajectories of modern insect lineages and ecological associations back in time to the Late Cretaceous.

Chapter 2: Insect herbivory on *Catula gettyi* gen. et sp. nov. (Lauraceae) from the Kaiparowits Formation (Late Cretaceous, Utah, USA)

Abstract

The Upper Cretaceous (Campanian Stage) Kaiparowits Formation of southern Utah, USA, preserves abundant plant, invertebrate, and vertebrate fossil taxa. Taken together, these fossils indicate that the ecosystems preserved in the Kaiparowits Formation were characterized by high biodiversity. Hundreds of vertebrate and invertebrate species and over 80 plant morphotypes are recognized from the formation, but insects and their associations with plants are largely undocumented. Here, we describe a new fossil leaf taxon, *Catula gettyi* gen et. sp. nov. in the family Lauraceae from the Kaiparowits Formation. *Catula gettyi* occurs at numerous localities in this deposit that represent ponded and distal floodplain environments. The type locality for *C. gettyi* has yielded 1,564 fossil leaf specimens of this species, which provides the opportunity to circumscribe the leaf shape, attachment, and venation patterns of this new plant morphospecies. In addition to describing the ecology of this taxon, including an extensive catalog of feeding damage on *C. gettyi* caused by herbivorous insects. We recorded more than 800 occurrences of insect damage belonging to five functional feeding groups indicating that insect-mediated damage on this taxon is both rich and abundant. *C. gettyi* is one of the best-sampled

host plant taxa from the Mesozoic Era, and its insect damage is comparable to other Lauraceae taxa from the Late Cretaceous.

Introduction

Lauraceae Juss. (Order Laurales) is a speciose and anatomically diverse family of aromatic magnoliid angiosperms. Today, the family is generally thought to consist of 45 genera and 2,850 species (Christenhusz and Byng 2016) to perhaps as many as 52 genera and 3,500 species (Rohwer 1993b). The Lauraceae are almost exclusively trees and shrubs, although species in the genus *Cassytha* L. may exhibit herbaceous or parasitic growth forms (Rohwer 1993b, Weber 1981). The family is mostly evergreen and occupies ecologically important roles in tropical and warm-temperate forests across a significant altitudinal range (Reis-Avila and Oliveira 2017, van der Werff and Richter 1996). Economically important genera in the Lauraceae include *Persea* Mill. (avocados), *Cinnamomum* Schaeff. (cinnamon), *Laurus* L. (bay laurel), and *Umbellularia* Nuttall (California bay). Leaves of Lauraceae are often dark green and glossy on their adaxial surfaces and villous and grey-green on their abaxial surfaces (Rohwer 1993b). Notably, the leaves are often leathery, which improves their preservation potential in the fossil record.

The Lauraceae has a particularly good fossil record compared to other major dicot lineages. The oldest unequivocal occurrence of reproductive organs attributed to the Lauraceae are charcoalified flowers of *Potomacanthus lobatus* von Balthazar et al. (2007) from the Potomac Group, a Lower Cretaceous deposit (ca. 108 Ma), from eastern North America. The oldest fossil leaves assigned to Lauraceae are of similar

age. They include examples such as those from the from the Dakota Formation (ca. 102 Ma), described as *Rogersia dakotensis* Wang and Dilcher (2018), *Wolfiophyllum heigii* Wang and Dilcher (2018), *Pandemophyllum* Upchurch and Dilcher (1990), and *Pabiana* Upchurch and Dilcher (1990). In Upper Cretaceous strata, fossil occurrences of Lauraceae are abundant and worldwide. Notable examples include 1) charcoalified flowers, peduncles, fruits, and stems of *Mauldinia* sp. from the Vocontian Basin in southeastern France (ca. 97 Ma) (Moreau et al. 2016); 2) carbonized flowers and inflorescences of *Mauldinia bohemica* Eklund and Kvaček (1998) from the Peruc-Korycany Formation (ca. 95 Ma) in the Czech Republic; 3) carbonized flowers of *Perseanthus crossmanensis* Herendeen et al. (1994) of the Raritan Formation (ca. 91 Ma), New Jersey, U.S.A.; and 4) wood of *Paraphyllanthoxylon vancouverense* Jud et al. (2018) from the Comox Formation (ca. 89 Ma) in British Columbia, Canada . By the latest Cretaceous, taxa attributable to Lauraceae are found in many deposits bearing abundant fossil leaves. For example, *Marmarthia trivialis* Johnson (1996) and *Marmarthia pearsonii* Johnson (1996) from the Hell Creek Formation (ca. 67.5-66 Ma) of the Williston Basin, North Dakota, USA, are widespread within the upper third of the rock unit.

Alongside inferences from molecular diversification proxies, fossil occurrences of Lauraceae indicate that the family evolved and began to diversify in the Early Cretaceous. Furthermore, fossil attributions indicate that the family was substantially diverse by the end of the Cretaceous (Chanderbali et al. 2001, Michalak et al. 2010, Tank et al. 2015). However, evidence for Cretaceous diversification of the family is limited compared to the Cenozoic diversity of Lauraceae (von Balthazar et

al. 2007). Additional research on the taxonomy and ecological associations of Cretaceous Lauraceae will assist paleobotanists as they map the evolution of this important angiosperm family in time and space.

Due to several field campaigns since the 1990s, the biota of the Kaiparowits Formation (Upper Cretaceous, 76.6–74.5 Ma (Roberts et al. 2013)) is increasingly well known (see Titus et al. 2016, Titus and Loewen 2013). Fossils from this formation number in the thousands and are present in several major museum collections in the United States. Dinosaurian and associated vertebrate fauna, as well as aquatic and infaunal invertebrates, have been extensively described in *At the Top of the Grand Staircase: The Late Cretaceous of Southern* Utah, edited by Titus and Loewen (2013). Large collections of megafossil plants, including leaves and wood, and palynoflora have been collected and are presently being described (Miller et al. 2013). The stratigraphy, sedimentology, and geochronology of the formation are increasingly well understood (Crystal et al. 2019, Roberts 2007, Roberts et al. 2005, Titus and Loewen 2013). Despite this growing body of work, insects, the most diverse group of animals and a cornerstone of terrestrial ecosystems, have not received much attention. Insect body fossils are poorly known worldwide from the Campanian (83.6—72.1 Ma) (Labandeira 2006b), particularly when compared with insect amber and compression-impression deposits from ca. 120 to 90 Ma (Grimaldi and Engel 2005, Ross 2015). Except for social insect nests (Roberts and Tapanila 2006), and dermestid beetle bone borings (Roberts et al. 2007), the diversity and ecological roles of Kaiparowits Formation insects, such as detritivores, predators and their prey, parasitoids, and herbivores are largely unknown. This provides an

opportunity to use insect-damaged leaves as a proxy for the guilds of herbivorous insects that existed in this ecosystem.

The first paleobotanical exploration of the Kaiparowits Formation began in the late 1990s (Titus and Loewen 2013). The approach taken by the Denver Museum of Nature & Science (DMNS) team was to discover and extensively quarry sites with well-preserved fossil leaves to build a comprehensive collection of plant taxa as a baseline for future work. One highly productive locality (Lost Valley, DMNH loc. 4150), yielded more than 4,000 identifiable leaf fossils, all of which were collected and housed at DMNS. This collection included more than 1,500 specimens of the leaf morphospecies described in this paper, providing a rare opportunity to analyze insect damage on a very large sample of leaves from a single species. Using these fossils, we describe a new species within the family Lauraceae and document the evidence of plant–insect interactions on this new species as an indicator for the richness and intensity of insect herbivory within the middle Kaiparowits ecosystem. The aims for this study are threefold: 1) Describe and name the new taxon based on fossil leaves; 2) measure the richness and intensity of insect damage on the new taxon; are 3) compare the richness and intensity of insect damage to that of other Late Cretaceous taxa attributed to Lauraceae.

Geologic and Biologic Setting

The Kaiparowits Formation is located in south-central Utah, USA, largely within the newly diminished boundaries of the Grand Staircase-Escalante National Monument (Figure 2.1). The formation comprises ~1005 m of alternating sandstone

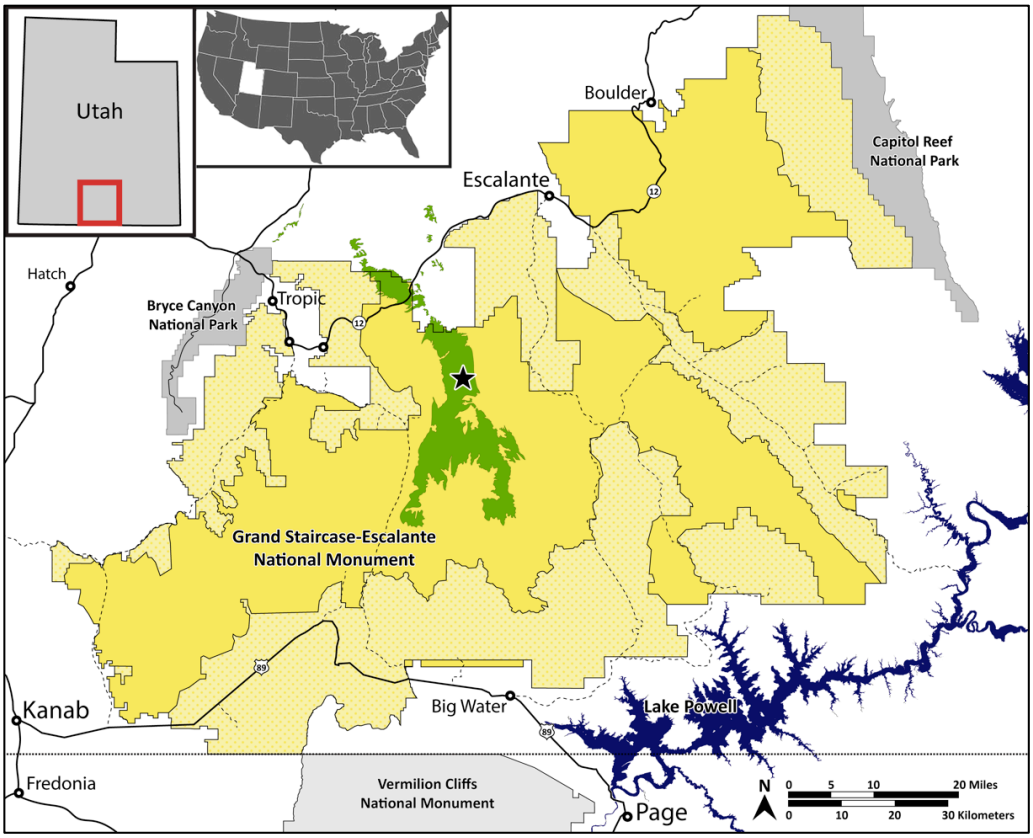


Figure 2.1. Map of the Grand Staircase-Escalante National Monument and the Kaiparowits Formation outcrop (green). Solid yellow denotes new monument boundaries (December 2017) and former monument areas are stippled in lighter yellow. DMNH loc. 4150, the Lost Valley locality, is denoted by a star. Adapted from Crystal et al. (2019).

and mudstone beds from an array of depositional environments, including channels, lakes, and a variety of floodplain deposits that include crevasse splays, perennial ponds, and oxbow lakes (Roberts et al. 2005, Roberts et al. 2013) (Figure 2.2). The depositional environment of the Kaiparowits Formation is interpreted as an alluvial to coastal plain, with source material originating from the west along the Sevier orogenic belt and directed to the Western Interior Seaway in the east. $^{40}Ar/^{39}Ar$ dating from the Kaiparowits Formation provides an age of ~76.6–74.5 Ma (Roberts et al. 2013), placing it within the Campanian Age (83.6 to 72.1 Ma) of the Upper Cretaceous. Penecontemporaneous formations include the Dinosaur Park Formation

in Alberta, Canada, and the Two Medicine and Judith River formations of Montana, USA, among other paracontemporaneous formations from Mexico to Alaska. The paleoenvironment likely was extensively ponded and annually flooded, based on the paludal deposits, floral and faunal composition, leaf physiognomy (Miller et al. 2013), and isotopic composition of dinosaur teeth (Crystal et al. 2019). This interpretation, along with temperature estimates from fossil leaves, suggests the climate was humid and subtropical, similar to the present-day Gulf Coast or certain areas of Southeast Asia (Miller et al. 2013, Roberts 2007).

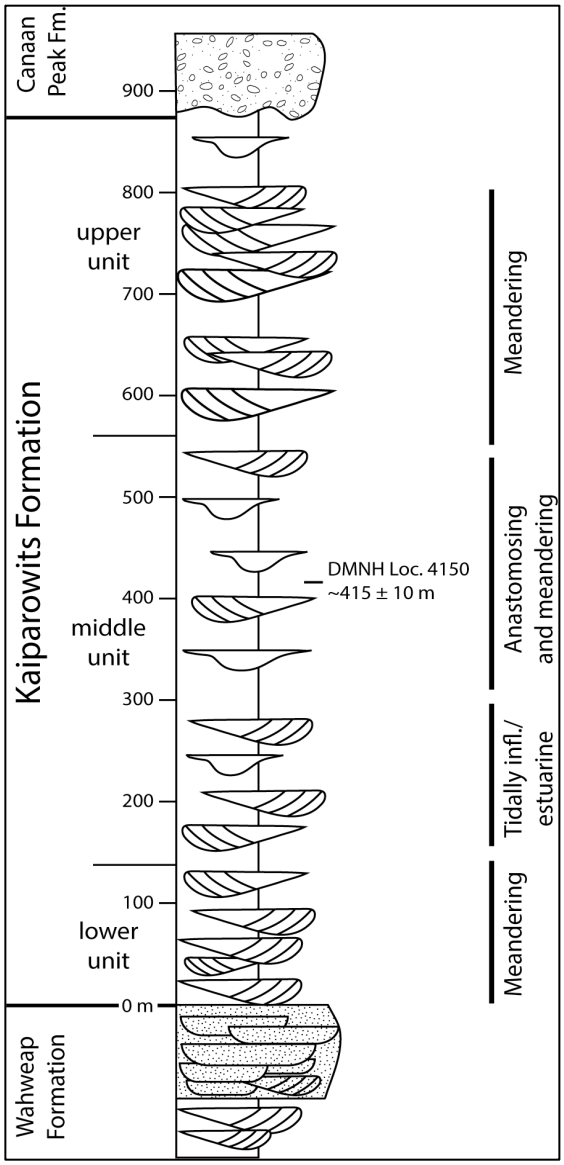


Figure 2.2: Representative stratigraphic column for the Kaiparowits Formation redrawn from Roberts (2007) showing major sedimentary modes. The stratigraphic position of DMNH loc. 4150, where the type and referred material for *C. gettyi* was collected, was located by directly measuring section from the contact with the Wahweap Formation with the assistance of J. Hagadorn and M. Marshall in 2015.

The Kaiparowits Formation is informally divided into upper, middle, and lower units, as well as the newly described Upper Valley Member (Beveridge et al. 2020), with the middle unit producing the bulk of floral and faunal specimens. During the past ten

years of field exploration, the authors have found and collected more than 100 megafloral localities within the formation. Most of these localities occur in the middle unit, which ranges stratigraphically from about 90–110 m at its base to about 550 m at its uppermost level within the formation (Roberts 2007). For the middle unit, the majority of megafloral localities are restricted to the stratigraphic interval between about 300 m and 450 m (Miller et al. 2013). Based on correlation to the local stratigraphic section for the Fossil Ridge area (Roberts et al. 2013), the Lost Valley Locality (DMNH Loc. 4150), is located in the middle unit of the Kaiparowits Formation, approximately 415 ± 10 m above its base. Using a depositional rate of 41 cm/1,000 years (Roberts et al. 2013), which was calculated using $^{40}Ar/^{39}Ar$ ages on sanidine crystals from volcanic ash beds, we estimate the age of DMNH Loc. 4150 at 75.6 ± 0.18 Ma. The error of this estimate was propagated from the error associated with the age on the nearest ash bed (Death Ridge Ash, (Roberts et al. 2013)) and the stratigraphic positions of the ash bed and the fossil locality.

At DMNH Loc. 4150, leaves are preserved as compression-impression fossils in stacked 5–10 cm thick, fine-grained sandstone beds with minor mud partings. The depositional environment is interpreted as a medial to distal crevasse splay resulting from an event or events that infilled a perennial pond or small lake. Using the facies associations of Roberts (2007), the fossils occur in the FA5 stratum, which consists of minor tabular and lenticular sandstone, immediately above the FA9 stratum, which is carbonaceous mudstone. FA5 is interpreted as forming from crevasse splays and crevasse channels, whereas FA9 is interpreted as forming in swamp and oxbow lake environments (Roberts 2007).

Materials and Methods

The plant megafossils from the Lost Valley locality (DMNH loc. 4150) were collected using standard bench-quarrying techniques. We collected all identifiable specimens and did not make a field census because the flora had not been previously sorted into morphotype categories. In the lab, the megafossils were sorted into morphotypes following the concept and procedure described by Johnson (1989). This method uses the morphological characters of disassociated plant organs, such as leaves, fruits, and stems, to circumscribe discrete operational taxonomic units prior to erection of a formal taxonomy. These morphotypes, based on multiple, well-preserved specimens, closely approximate biological species. We use the morphotype prefix, KP, to designate the Kaiparowits Formation, followed by a sequential listing of the number of morphotypes in the formation (see Miller et al. 2013).

The Lost Valley locality (DMNH loc. 4150) contains 4,004 specimens identified to 101 morphotypes. The non-reproductive morphotypes include 8 ferns, 1 lycopod, 1 sphenopsid, 1 gymnosperm, and 59 angiosperms. The reproductive morphotypes include 31 seeds, fruits, and flowers. Of all specimens from this locality, 1,564 (~39%) were assigned to KP89 and formally described and named below. Specimens of KP89 that were more than a third complete were examined for insect-mediated damage. The majority of specimens were over fifty percent complete. A formal description of this taxon was erected to 1) advance our understanding of the Kaiparowits Flora; 2) provide a foundation for ecological analyses, described below;

and 3) allow for comparisons of specialized plant–insect associations between other, described Lauraceae taxa from the Late Cretaceous of North America.

Insect herbivory was documented following a system of identification and classification frequently employed in plant–insect associational studies (Currano et al. 2010, Currano et al. 2008, Donovan et al. 2016, Donovan et al. 2014, Labandeira et al. 2002a, Labandeira et al. 2002b, Labandeira et al. 2007c, Wilf and Labandeira 1999). There are several criteria used to distinguish herbivore induced insect damage from other types of damage, such as physical damage resulting from tears occurring along leaf veins, detritivory involved in the consumption of dead tissue, or taphonomic processes that alter leaf tissue. The first criterion is the presence of reaction tissue. Reaction tissue often occurs as anomalous parenchymatous enlargement, such as callus, that results from hypertrophic (enlarged) or hyperplasic (multiplied) cells produced by the plant along insect damaged areas (Brues 1924, Johnson and Lyon 1991, MacKerron 1976, Vincent et al. 1990). A second criterion for insect damage is the targeting of a specific host-plant taxon or a particular plant organ that would be attributable to insect-specific patterns of damage. Examples of this type of damage are linear rows of punctures on or along primary veins, or small cusps occurring on the cut edge of a plant tissue (Gangwere 2017, Iannuzzi and Labandeira 2008, Kazakova 1985, Keen 1952). A third criterion is a repeated damage pattern based on shape, size, and position of the damage on the plant (Bodnaryk 1992, Heron 2003). After herbivore mediated damage was identified on the plant host, it was classified by feeding guild, or functional feeding group, and into specific,

diagnosable patterns of insect plant-tissue modification, the damage type (Labandeira et al. 2007c).

Insect damage was scored following the *Guide to Insect (and other) Damage Types on Compressed Plant Fossils* (Labandeira et al. 2007c) and subsequent published and unpublished addenda. The damage was initially categorized into one of eight functional feeding groups: 1) hole feeding; 2) margin feeding; 3) surface feeding; 4) skeletonization; 5) piercing and sucking; 6) oviposition; 7) galling; and 8) leaf mining. Oviposition is not herbivory per se, but does represent damage to the foliar tissue of plants that elicits defense responses and has a persistent fossil record (ex. Gnaedinger et al. 2014, Laaß and Hoff 2015, Lin et al. 2019, Meng et al. 2019, Moisan et al. 2012, Vasilenko 2008). Similarly, galls may be created by insects, mites, nematodes, fungi, bacteria, or viruses (Mani 1964). Galls may be formed in conjunction with oviposition or maturation and may or may not be associated with herbivory (Meyer 1987), but are herein categorized as insect damage. Discrete, diagnosable damage types were documented within each functional feeding group and assigned a damage type (DT) number. Damage types are specifically defined, diagnosable effects of insect feeding on plants that are classified by the shape, size, extent, and location of herbivore damage on the affected leaf (Labandeira et al. 2007c). Damage types are rated for host specificity: 1 or generalized (polyphagous), 2 or intermediate (oligophagous), and 3 or specialized (monophagous) (Labandeira et al. 2007c). The convergence of herbivore mouthparts and feeding behaviors make genus or species level identifications of the insect culprit rare. Except for some margin feeding, most leaf mines, most galls, and many scale-insect feeding marks

that are traceable to lineages with living representatives (ex. Jud and Sohn 2016, Sarzetti et al. 2008, Wappler and Ben-Dov 2008, Wilf et al. 2000, Winkler et al. 2010).

Herbivory data collected from insect damaged leaves includes both qualitative and quantitative data. The qualitative data, outlined above, determine the overall insect feeding guilds on a particular host-plant taxon, the richness of damage types, host specificities, and occasionally identities of the phytophagous insect responsible for the damage (see Chapter 4). Quantitative data collection consisted of three basic metrics: 1) the proportion of damaged leaves, 2) the richness of damage types, and 3) the percent of surface area herbivorized by insects (herbivory index). For calculating the surface area of leaf tissue herbivorized by insects, a subset of 156 specimens of the new taxon (10% of total specimens) was randomly selected using the random number generator package "Rando" for R statistical software (R Development Core Team 2013).

Four additional taxa attributed to the family Lauraceae from the Hell Creek Formation by Johnson (2002) were included in the final analysis: *Marmarthia pearsonii* (DMNH loc. 900), *Marmarthia trivialis* (DMNH loc. 428), "*Artocarpus*" *lessigiana* (DMNH loc. 428), and "*Ficus*" *planicostata* (DMNH loc. 428) (Hartman et al. 2002, Johnson 2002). Each Hell Creek Formation taxon with a sample size of at least 20 specimens from a single locality was analyzed for insect damage as outlined above. Comparisons were made to these taxa to provide context for the level of

herbivory on the Kaiparowits laurel described herein, as well as to determine if there are any specialized damage types that persist throughout the Late Cretaceous.

Detailed photographs were taken using a Canon EOS 50D camera with a Canon EF-D 60mm f/2.8 macro lens and microphotographic images were taken using an Olympus DP25 camera attached to an Olympus SZX12 microscope. Digital images were processed using Adobe Photoshop CC® (2017.01) and Zerene Stacker® software. Surface area for all five taxa in this study was measured using Adobe Illustrator Draw© for iPad Pro and ImageJ (Rasband 2012). Plates were created using Adobe InDesign CC® (2017.1).

Sample-based rarefaction was calculated for the damage type richness and sampled surface areas of the plant hosts, as it allows for comparisons of insect damage richness between taxa. Rarefaction by total sampled surface area was used instead of number of specimens because this standardizes differences in leaf size and leaf completeness between species. A rarefaction analysis and curve were created using code developed by S. Schachat (Schachat et al. 2018, Schachat et al. 2020) for R statistical software (R Development Core Team 2013). Rarefaction curves were bootstrapped 5,000 times to generate 95% confidence intervals. Herbivory index was calculated for the Hell Creek and Kaiparowits taxa and 95% confidence intervals were bootstrapped 10,000 times.

Nonmetric multidimensional scaling (NMDS) ordinations, which used a Bray-Curtis dissimilarity matrix, were produced via the metaMDS function of the vegan package, in R version 3.1.2 (R Development Core Team 2013), also used in previous studies (Maccracken and Labandeira 2020, Schachat et al. 2015). NMDS plots

represent the positions of data in multidimensional space and allow for visual comparisons between plant hosts. The NMDS plot was produced with the R package ggplot2 (R Development Core Team 2013). To standardize for sampling effort and to quantify uncertainty, each of the Kaiparowits and Hell Creek taxa were subsampled 500 times to a given amount of surface area. This process was repeated nine times, setting the seed in R from 1 to 9. For the first series of NMDS plots, all five taxa were subsampled to 850 cm^2 of surface area; "*A.*" *lessigiana* is represented by 884.85cm^2 of surface area. For the second series of NMDS plots, "*A.*" *lessigiana* was removed from the dataset and the remaining four taxa, which are represented by between 1420.36 and 1707.48 cm^2 of surface area, were subsampled to 1400 cm^2 of surface area. Ellipses contain 84% of points closest to the centroid of each taxon and represent 84% confidence intervals.

Results

Leaf Morphology and Systematics

Leaves of the new fossil taxon are herein described based on specimens exhibiting a range of vein preservation, leaf arrangement and attachment, and leaf shape. A formal description is forthcoming in a peer-reviewed journal and all future work citing this new genus and species should reference that publication (Maccracken et al. in review-a).

SYSTEMATICS

Order: Laurales (Juss. ex Bercht. & Presl, 1820)

Family: Lauraceae (Jussieu, 1789 *nom. cons.*)

Catula Maccracken, Miller, Johnson, Sertich, Labandeira, gen. nov.

Generic diagnosis. Leaves simple; when attached, distichous, exhibiting opposite or slightly subopposite arrangement and axillary buds. Lamina primarily ovate, occasionally elliptic, or rarely obovate; nearly always slightly asymmetrical in the apex, middle, and base of the leaf. Overall, leaves are highly variable in length, width, and size leading to considerable variation in shape. Leaf margin entire and unlobed. A fimbrial vein observable in well-preserved specimens. Leaf apex typically acute and often exhibiting a mucronate termination. Leaf base typically acute and markedly decurrent, with laminar tissue extending down the petiole. Primary venation pinnate. Secondary venation simple brochidodromous; associated with simple agrophic veins. Secondary veins basally crowded to form 1 or 2 pairs of acute basal secondary veins. Tertiary venation opposite percurrent with a variety of courses and an inconsistent angle relative to the primary vein. Exterior tertiary veins and ultimate observable venation looped. Higher order venation more or less disorganized and the leaf rank is 2r. Quaternary vein fabric regular to irregular reticulate and quinternary vein fabric irregular reticulate. No cuticular or fertile material has been recovered or associated with these leaf fossils.

Derivation of the generic name. From the masculine noun *catulus*, a Classical Latin noun meaning a young animal (Pliny), especially a young dog, puppy or whelp (Cicero, Lucretius, Vergil). The genus epithet is, in part, named for Mike Getty's dog, Javelina, who also answers to the name, Puppy. The diminutive suffix *–ulus*/*-a* also describes the small size of many of the leaves in this genus.

Catula gettyi Maccracken, Miller, Johnson, Sertich, Labandeira, sp. nov.

Figures 2.3 A–E, 2.4 A–C, Supplementary Figure 2.1 A–G.

Specific diagnosis. Same as the generic diagnosis by monotypy.

Holotype. Designated here: DMNH 54376 (Figure 2.3 A–E).

Paratypes. Designated here: DMNH 54378 (Figure 2.4 A, B – stem with many attached leaves), DMNH 54377 (Figure 2.4 C – stem with 3 attached leaves), DMNH 41570 (Supplementary Figure 2.1 A – single leaf), DMNH 54371 (Supplementary Figure 2.1 B – single leaf) DMNH 54379 (Supplementary Figure 2.1 C – single leaf) DMNH 54370 (Supplementary Figure 2.1 D – single leaf) DMNH 41584 (Supplementary Figure 2.1 E – single leaf) DMNH 41567 (Supplementary Figure 2.1 F – single leaf) DMNH 54380 (Supplementary Figure 2.1 G – single leaf).

Other figured specimens. Figures 2.7 – 2.14

Derivation of the specific epithet. In recognition of Michael A. Getty for his nearly two decades of incredible support and leadership in uncovering the paleontological treasures of Grand Staircase-Escalante National Monument.

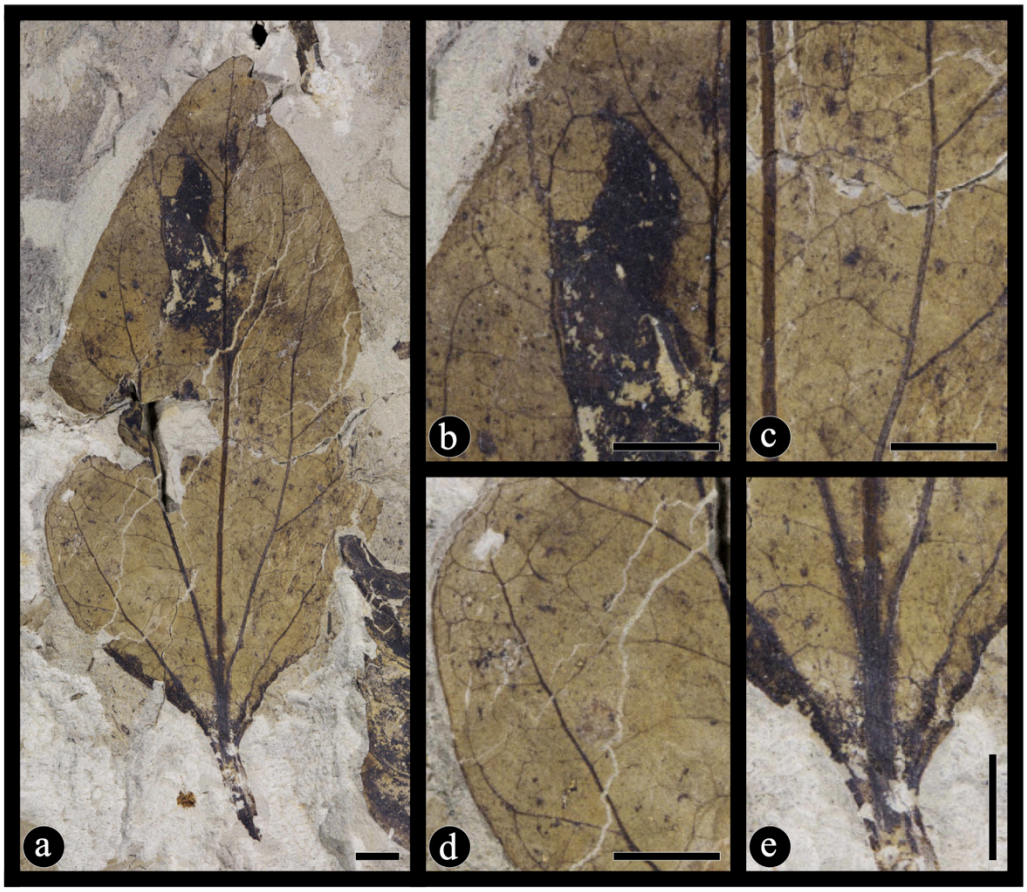


Figure 2.3 (A–E): Overall and detail images of the holotype specimen (DMNH 54376, DMNH loc. 4150) of *Catula gettyi* Maccracken et al. gen. et sp. nov. (A) Complete leaf. (B) Detail showing upper left section of the leaf with looping and simple brochidodromous secondary venation. The dark area on the leaf is a blotch mine. The primary vein of the leaf parallels the right side of the figure. (C) Detail showing a medial section on the right side of the leaf, with the primary vein on the left side of the figure. Note the epimedial tertiary veins with variable course, and the irregular to regular reticular quaternary venation. (D) Detail showing lower left section of the leaf with simple agrophic veins, looping ultimate marginal venation, and a fimbrial vein. (E) Detail showing the base of the leaf with 2 pairs of acute basal secondary veins and laminar tissue extending down the petiole. Note the decrease in the primary vein width with the departure of the secondary veins. All scale bars = 0.5 cm.

Source, age, and stratum. *Catula gettyi* is found throughout middle unit of the Kaiparowits Formation spanning perhaps as much as 1 myr. All *C. gettyi* specimens are housed at the Denver Museum of Nature & Science. Precise GPS locality information is available upon request.

Description. *Catula gettyi* occurs mostly as isolated leaves, while a few specimens show leaves attached to stems. Leaf attachment petiolate; leaf arrangement opposite to subopposite, appearing distichous; even and odd pinnate terminus on the stem; leaf organization simple. Auxiliary buds present in leaf axils. Petiole twisted, sometimes flanked with a thin wing of laminar tissue from the blade; petiole base slightly swollen. Blade attachment marginal. Laminar size notophyll, rarely nanophyll to mesophyll; laminar length variable but generally 4 to 8 cm; laminar width variable but generally 2.5 to 4.5 cm; laminar length to width ratio generally 1:1.0 to 3:1; laminar shape ovate or occasionally elliptic, or rarely obovate; medial symmetry slightly asymmetrical, rarely symmetrical. Laminar base slightly asymmetrical, rarely symmetrical, occasionally with a slight asymmetrical basal insertion; base angle acute; base shape decurrent. Laminar apex angle acute, rarely obtuse; apex shape straight to acuminate; laminar apex with a mucronate termination in some specimens, otherwise appearing slightly retuse. Leaf margin entire, unlobed; laminar edge appearing thickened or with an observable fimbrial vein of tertiary or higher order; laminar surface texture appearing smooth. Primary venation pinnate; thickness of primary vein up to ~1.3mm; course of primary vein approximately straight; primary vein markedly decreases in width after giving rise to major secondary veins, particularly near the base of the leaf. Secondary vein organization simple brochidodromous; agrophic veins present, simple; 1–5 or rarely 7 basal veins including both primary and secondary veins; naked basal veins present, of secondary or tertiary vein order; spacing of secondary veins on primary vein decreases proximal to the leaf base, forming 1 or 2 pairs of acute basal secondary veins; typically 4 pairs

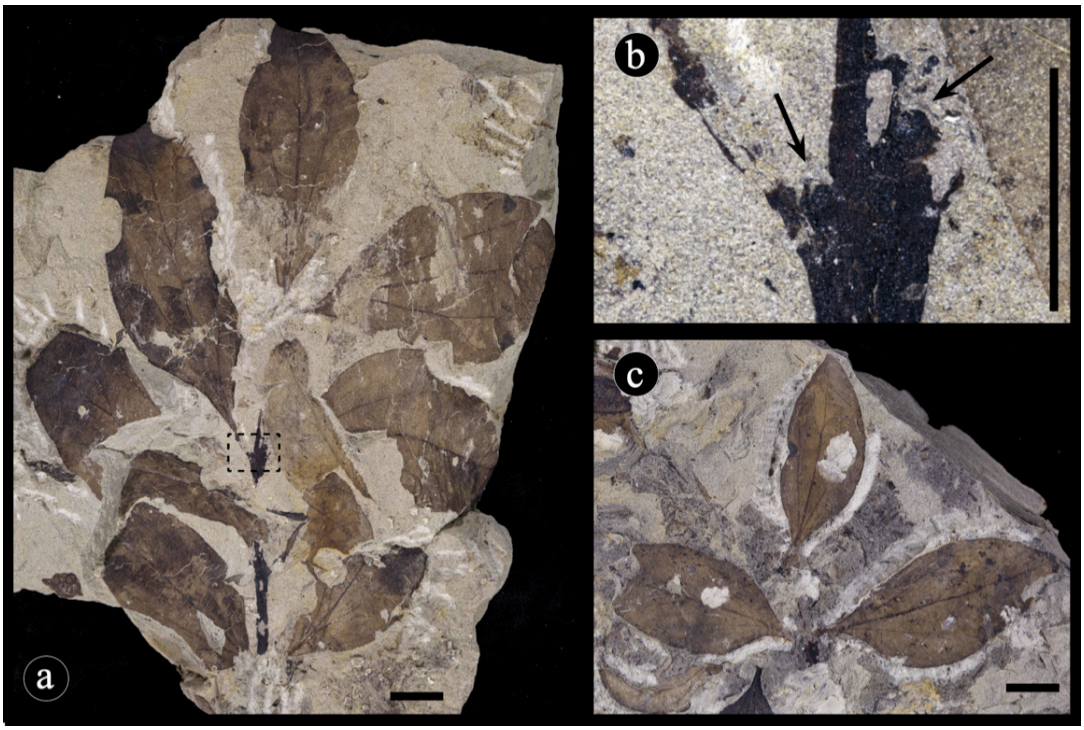


Figure 2.4 (A–C): Paratype specimens of *Catula gettyi*. (A) Attached leaves of *C. gettyi* on a stem showing opposite leaf attachment, probable distichous arrangement, and an odd-pinnate leaf terminus (DMNH 54378). Scale bar = 1 cm. (B) Enlarge section of dashed inset box in Figure 2.4 a showing leaf attachment (DMNH 54378). Arrows highlight axillary buds. Scale bar = 0.5 cm. (C) Attached leaves of *C. gettyi* on a stem showing opposite leaf attachment and an odd-pinnate leaf terminus (DMNH 54377). Scale bar = 1 cm.

of secondary veins; angle of secondary vein departure from primary vein acute; secondary vein course generally arching towards leaf apex, decurrent on the primary vein, course deflected at the origin of minor secondary veins; minor secondary vein course simple brochidodromous; interior secondary veins absent; intersecondary veins absent. Intercostal tertiary vein organization opposite percurrent and sinuous to convex; tertiary vein course angle with respect to the primary vein acute; tertiary vein angle variability with respect to the primary vein inconsistent. Epimedial tertiary veins alternate percurrent; proximal course acute to the midvein, distal course basiflexed. Exterior tertiary course looped. Quaternary vein fabric regular to irregular

reticulate. Quinternary vein fabric irregular reticulate. Higher order venation obscured. Marginal ultimate venation appearing looped. No cuticular or fertile material recovered or associated with these leaf fossils.

Remarks. We compared the *Catula gettyi* specimens to Cretaceous through Eocene leaves (e.g. Berry 1925, Brown 1962, Hickey et al. 2006, Johnson 1996, 2002, Knowlton 1900, Lesquereux 1878, Manchester 2014). Despite the abundance of fossil "lauroid" leaves in the literature, we found few favorable matches. Of the fossils most similar to *C. gettyi* were fossils assigned to the extant genus *Cinnamomum* in the Lauraceae. In particular, "*Cinnamomum" newberryi* Berry (1925) and "*Cinnamomum" newberryi ellipticum* Berry (1925) from the Maastrichtian Ripley Formation in Texas are similar in many aspects to *C. gettyi* but differ by having a more narrow leaf shape, prominent agrophic veins and better organized opposite percurrent epimedial tertiaries with more or less straight courses. *"Cinnamomum" affine* Lesquereux in Knowlton (Knowlton 1900) from the Campanian Mesaverde Formation, and *"C." affine* Lesquereux (Lesquereux 1878) from the Maastrichtian Laramie Formation share characters with *C. gettyi* based on leaf shape and two pairs of acute, basal, secondary veins, but differ by exhibiting better organized opposite percurrent epimedial tertiaries with straight courses. The lauraceous taxon *Marmarthia pearsonii* Johnson (Johnson 1996) from the Maastrichtian Hell Creek Formation resembles *C. gettyi*, particularly from the perspective of higher order venation and overall low leaf rank. However, *M. pearsonii* differs from *C. gettyi* by having primary venation that is basal acrodromous as opposed to pinnate, only one pair of prominent basal veins (primary or secondary), more prominent epimedial

tertiary veins, and a naked base. Finally, *"Cinnamomum" linifolium* Knowlton (Knowlton 1917) from the Paleocene Raton Formation bears resemblance in overall shape and primary and secondary venation to *C. gettyi*, but the specimens are too poorly preserved for taxonomic comparison outside the formation.

We have assigned *C. gettyi* to Lauraceae based on the combination of the following characteristics. *Catula gettyi* has simple leaves, distichous and opposite or slightly subopposite leaf arrangement with axillary buds, entire margins, pinnate primary venation, simple brochidodromous secondary venation, and a markedly decurrent base with 1 or 2 pairs of acute basal secondary veins. While this set of characters is perhaps not unique to Lauraceae, we are confident, based on the current material, that the familial placement is warranted.

In Lauraceae, *C. gettyi* exhibits a leaf shape and primary, secondary, and tertiary venation consistent with species in extant *Cinnamomum* (see Klucking 1987). Several workers have argued that *Cinnamomum* exhibits two characteristic primary venation patterns (Hernandez 1997, Lorea-Hernandez 1997, Ravindran et al. 2003): acrodromous venation typified by *Cinnamomum verum* (cinnamon), and pinnate venation typified by *Cinnamomum camphora* (camphor). We examined herbarium sheets of 133 species of *Cinnamomum* (~38-53% percent of the 250 (Ravindran et al. 2003) to 350 (Rohwer 1993a) species) in the Smithsonian's National Museum of Natural History virtual botany collections and the New Botanical Gardens Steere Herbarium C.V. Starr Virtual Herbarium and found additional support for these venation patterns, plus a third pattern. These patterns are: 1) an acrodromous primary venation pattern that with weakly expressed brochidodromous to eucamptodromous

secondary veins and prominent, usually well-organized opposite percurrent tertiary veins. 2) A pinnate primary venation pattern with prominent basal secondary veins that have an acrodromous or brochidodromous course. In the distal portions of these leaves, additional well-defined brochidodromous secondary veins occur. Tertiary veins in this category are typically alternate percurrent to mixed opposite and alternate percurrent. And 3) a pinnate venation pattern that does not have prominent basal secondary veins. Secondary veins in this category are typically of the same gauge or are reduced in gauge uniformly from the base of the leaf to the apex. Tertiary veins in this category range considerably in course and organization.

Considering these venation patterns, *Catula gettyi* appears more closely allied with the "intermediate" category exhibiting pinnate venation with prominent basal secondary veins. The 15 most comparable taxa that we observed are listed in Supplementary Table 2.1 (Appendix B). While *C. gettyi* compares favorably to these taxa, there are notable differences in vein organization. Collectively, these differences show that the veins of *C. gettyi* are less organized, leading to an overall lower leaf rank (Hickey and Doyle 1977), than any taxa we observed in *Cinnamomum*. Given the poorly organized leaf venation of *C. gettyi*, and without floral, epidermal, and petiolar/laminar (e.g. domatia) characters (e.g. Ravindran et al. 2003) to place the new taxon in *Cinnamomum*, we have elected to erect the new genus and species *Catula gettyi*.

Catula gettyi represents the single most abundant leaf megafossil found in the Kaiparowits Formation based on the current collection at the Denver Museum of Nature & Science. In many proximal crevasse-splay floras from the formation, *C.*

gettyi is the dominant taxon. While a comprehensive analysis of splay, channel, and pond floras in the formation has yet to be completed, it nonetheless appears that *C. gettyi* tracks stream margins, and thus disturbed, environments in the formation.

Insect Herbivory on *Catula gettyi*

We identified 40 distinct patterns of herbivore damage (DTs) on *Catula gettyi* leaves at Lost Valley (DMNH loc. 4150) (Table 2.1; Figure 2.5). A total of 863 damage-type occurrences were present and the percentage of *C. gettyi* leaves with at least one type of insect damage at this locality was 38.75% (606 damaged specimens, including some specimens with multiple damage types). For 156 randomly selected *C. gettyi* leaves, the herbivory index, or the percentage of herbivorized surface area is 2.102% (Figure 2.6). The 95% confidence interval ranges from 1.36% to 3.03%. Rarefaction was calculated for damage types and total sampled surface area (156 specimens subsampled, 2,985.841 mm^2).

Table 2.1: Richness of damage types by functional feeding group and host plant specialization on *Catula gettyi*. Abbreviations are: HF, hole feeding; MF, margin feeding; SK, skeletonization; SF, surface feeding; PS, piercing and sucking; OV, oviposition; LM, leaf mining; and GL, galling.

Host plant specificity	Damage Types								
	HF	MF	SK	SF	PS	OV	LM	GL	Total
Generalist	6	3	1	3	0	0	0	0	13
Intermediate	5	3	3	1	0	1	0	2	15
Specialist	0	0	1	0	4	0	5	2	12
Total	11	6	5	4	4	1	5	4	40

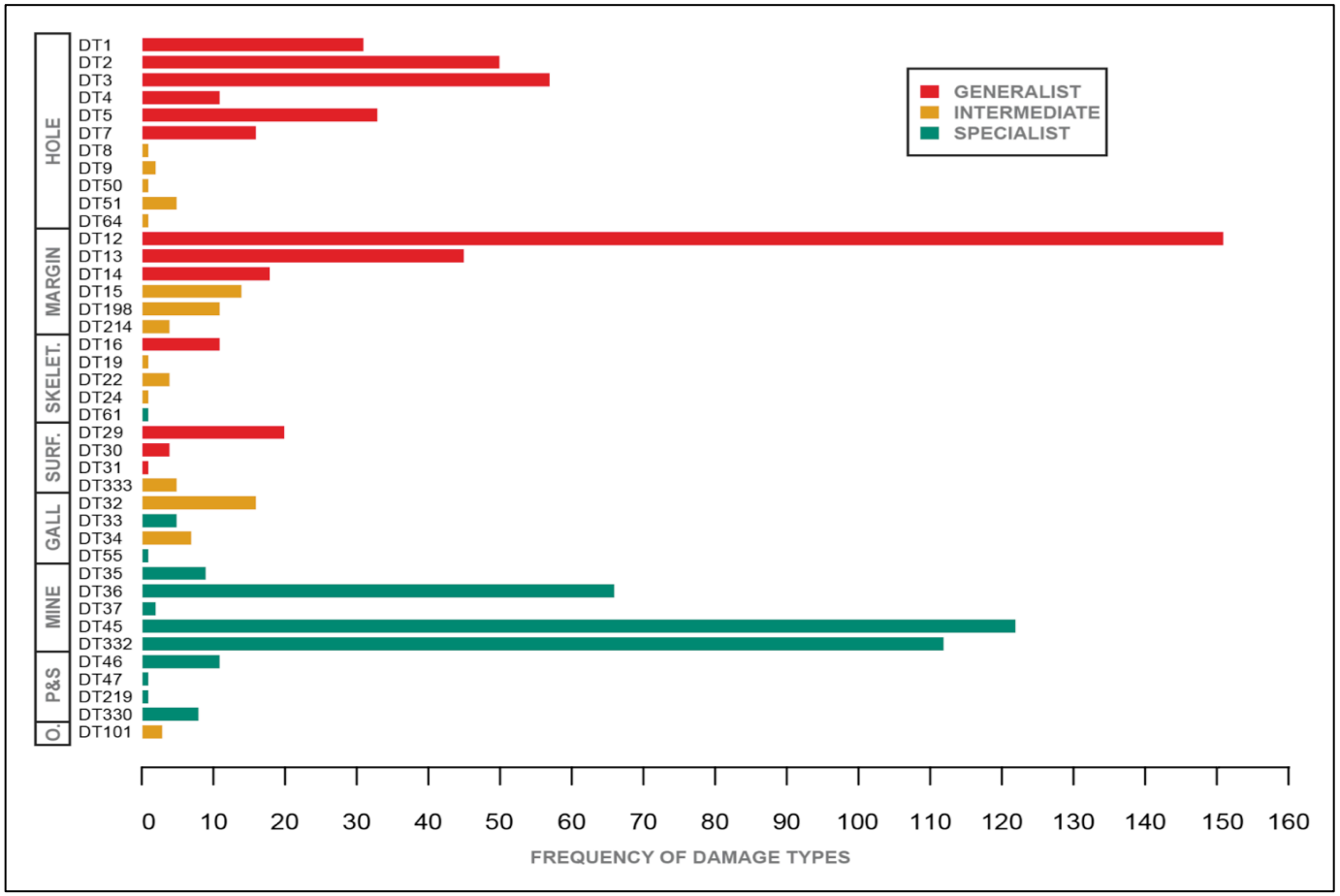


Figure 2.5: Histogram of all damage types encountered on *Catula gettyi* by functional feeding group. Red bars = generalist host specificity, gold bars = intermediate host specificity, and green bars = specialized host specificity.

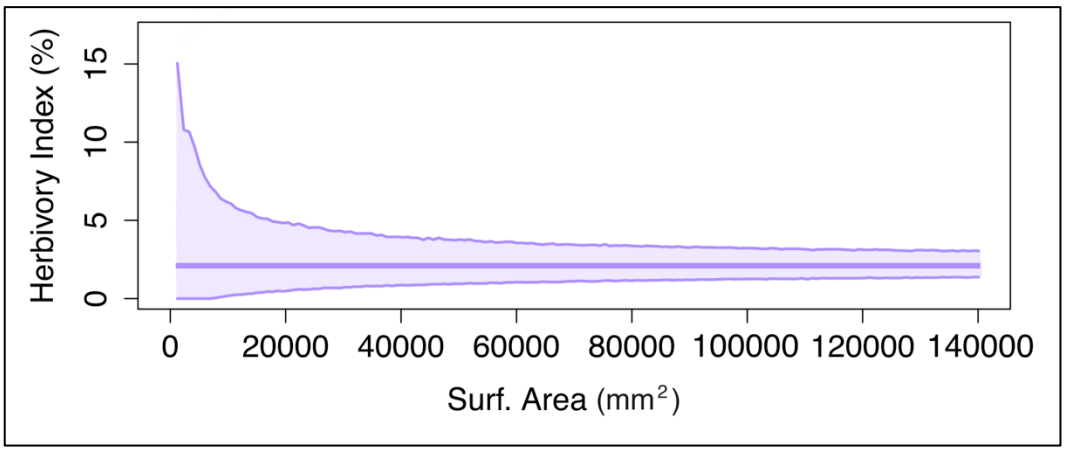


Figure 2.6: Herbivory index for the subsampled *Catula gettyi* dataset with 95% confidence intervals.

The ectophytic functional feeding groups of hole feeding, margin feeding, skeletonization, and surface feeding, were the most diverse and abundant modes of feeding on *C. gettyi*, with a total of 26 distinct damage types and 498 occurrences. There were 14 damage types and 365 damage-type occurrences of endophytic functional feeding groups (i.e. piercing and sucking, oviposition, mining, and galling) on *C. gettyi*. In addition, the presence of fungal necroses is commonly associated with insect herbivory; however, no clear insect-mediated fungal damage was encountered on *C. gettyi*, as it was difficult to distinguish fungus from discoloration associated with decay and burial. Fungus was most commonly found on poorly preserved and physically damaged specimens, which indicates that fungal attack occurred post-senescence.

Hole Feeding. — Hole feeding is the consumption of a leaf, which includes the entire thickness of the lamina and does not reach the leaf margin. Hole feeding on *Catula gettyi* is common and diverse, with eleven damage types and 207 occurrences of DT1, DT2, DT3, DT4, DT5, DT7, DT8, DT9, DT51 and DT64 (Figure 2.7). Circular hole

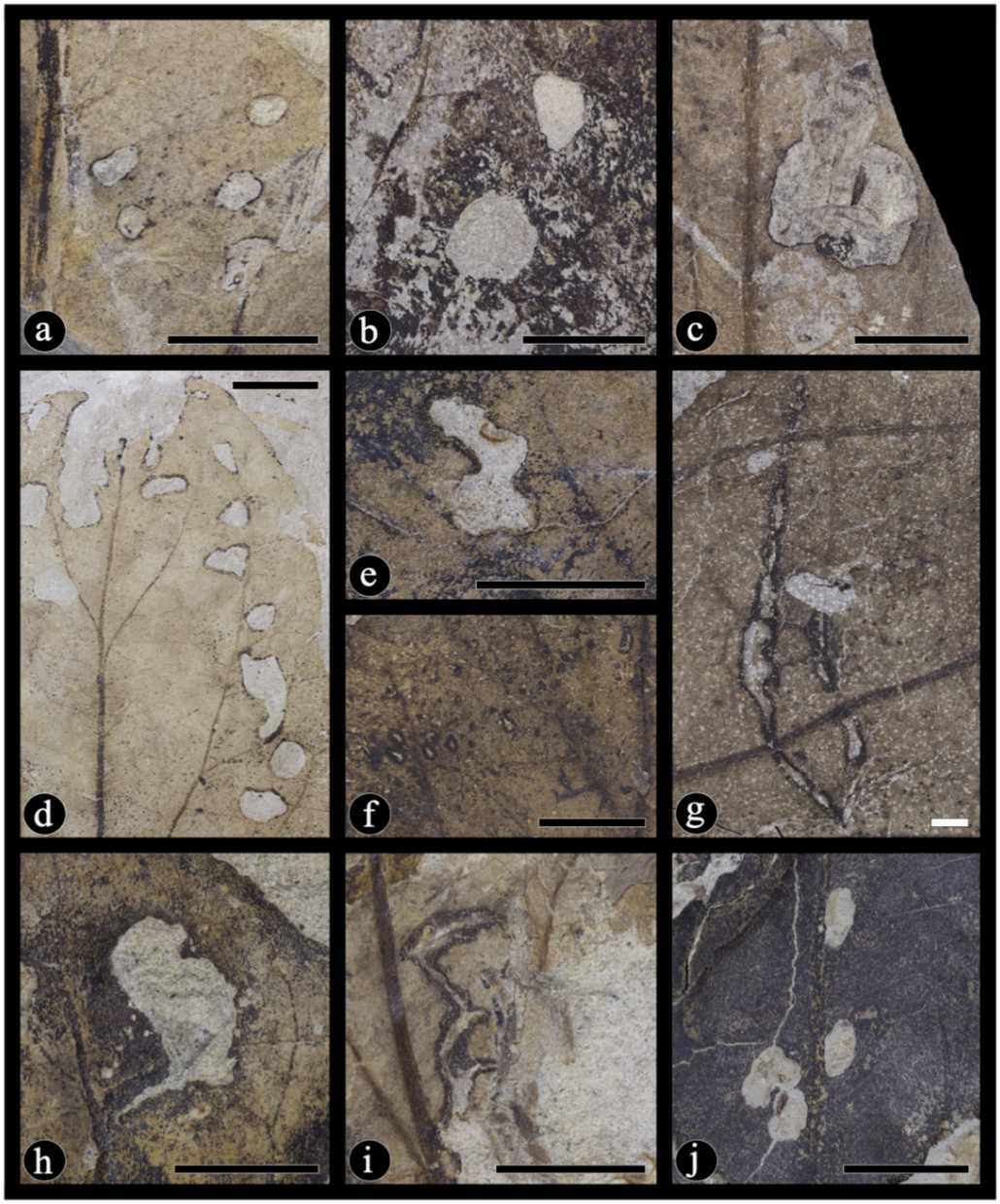


Figure 2.7 (A–J): Eleven hole-feeding damage types found on *Catula gettyi* produced by mandibulate insects: (A) DT1; Circular holes under 1mm in diameter (DMNH 41564); (B) DT2; Circular holes between 1 mm and 5 mm in diameter (DMNH 41580); (C) DT4; Circular holes greater than 5 mm in diameter (DMNH 41596); (E) DT3; Polylobate holes between 1 mm and 5 mm in diameter (DMNH 41576); and (H) DT5; Large polylobate holes over 5 mm in diameter (DMNH 41583). Less common hole-feeding types consist of (G) DT7 & DT8 (DMNH 41590); Rectilinear holes and slot feeding, respectively (DMNH 41590); (F) DT9; Scattered, comma-shaped holes (DMNH 39733); (D) DT64; Holes located along the margin of the leaf (DMNH 41584); (I) DT51; Overlapping slot feeding holes (DMNH 41571); and (J) DT50; A series of holes associated with a primary vein (DMNH 41574). Black scale bars= 5 mm; white scale bars= 1 mm.

feeding damage types include holes below 1 mm in diameter (DT1) (Figure 2.7 A), holes between 1 mm and 5 mm in diameter (DT2) (Figure 2.7 B), holes above 5 mm in diameter (DT4) (Figure 2.7 C), and a series of three or more circular holes along the leaf margin (DT64) (Figure 2.7 D). Polylobate hole feeding includes holes between 1 mm and 5 mm (DT3) (Figure 2.7 E), and holes over 5 mm in diameter (DT5) (Figure 2.7 H). DT7 are rectilinear feeding (Figure 2.7 G); DT51 consists of overlapping slot feeding (Figure 2.7 I); and DT9 are elliptical to comma-shaped holes scattered across the leaf surface (Figure 2.7 F). Finally, DT50 is a linear series of holes alongside a primary or secondary vein that occur on one side or on alternating sides (Figure 2.7 J).

Margin Feeding. — Margin feeding is the consumption of the entire thickness of the lamina along the leaf edge by a chewing phytophagous insect. The six distinct margin-feeding damage types on *C. gettyi* specimens are DT12, DT13, DT14, DT15, DT198 and DT214 (Figure 2.8). DT12 is the cuspate and moderately incised, and isolated removal of tissue at the leaf margin; it represents the most common damage type on *C. getty*i (Figure 2.8 C). DT13 is the removal of tissue at the leaf apex (Figure 2.8 B), whereas DT14 is the removal of leaf tissue along the margin and to the primary vein (Figure 2.8 A). DT15 is a deeper, trenched incision that is deeply incised and is parallel sided or expands towards the primary vein (Figure 2.8 D), whereas DT198 also is a deep incision but narrows medially (Figure 2.8 E). DT214 is a series of cuspate feeding traces with three or more, distinctively shaped, scalloped incisions (Figure 2.8 F).

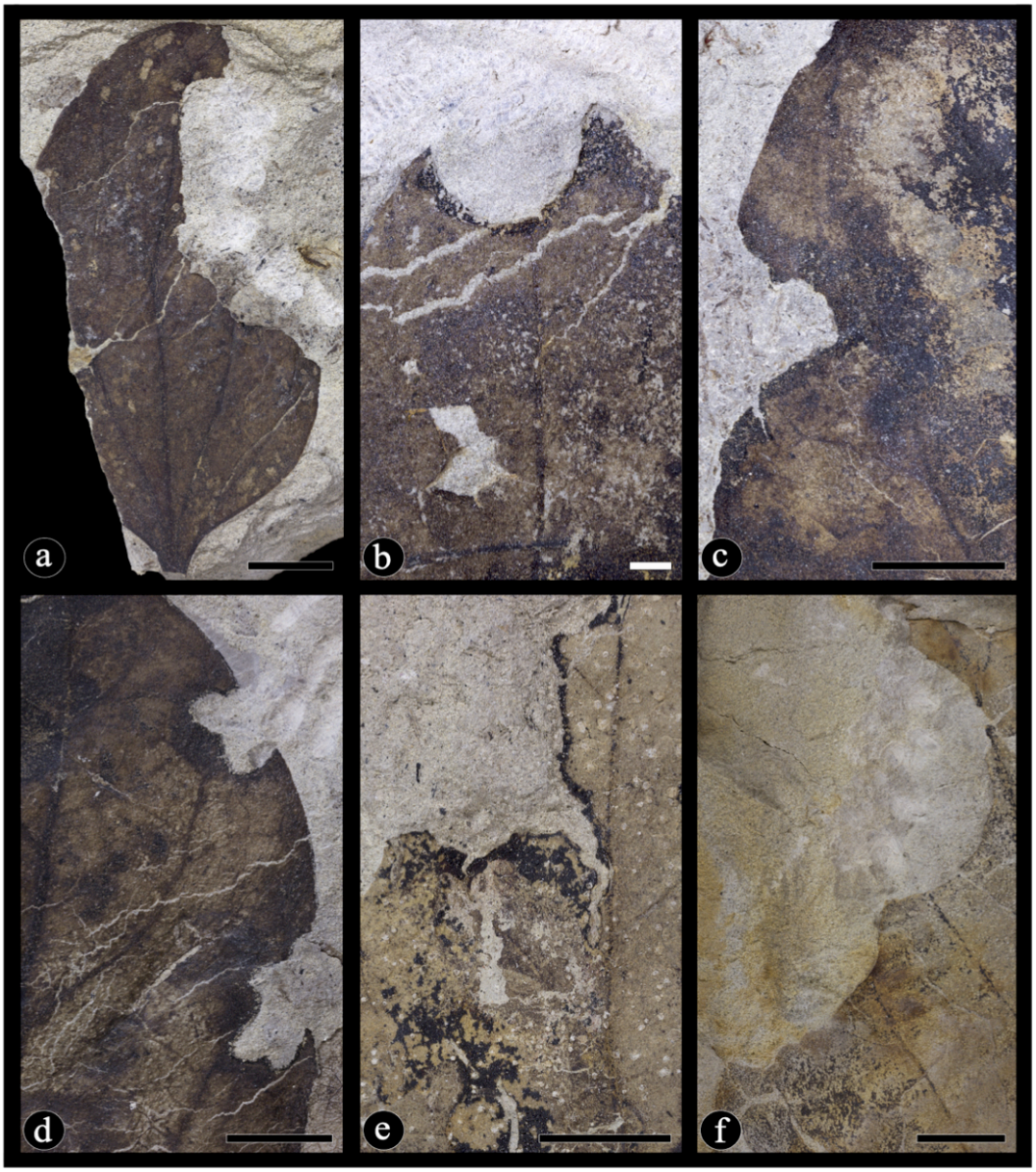


Figure 2.8 (A–F): Margin feeding damage types found on *Catula gettyi* at the Lost Valley Locality: (A) DT14; Excision of the leaf to the primary vein (DMNH 41575); (B) DT13; The removal of the apex of leaf by the insect (DMNH 41578); (C) DT12; A common semi-circular excision of the leaf margin (DMNH 41579); (D) DT15; An excision that expands medially (DMNH 41585); (E) DT198; A deep, narrow excision with broad reaction tissue surrounding the herbivorized section (DMNH 41595); and (F) DT214; Multiple, connected excisions along the leaf margin (DMNH 41586). Black scale bars= 5 mm; white scale bars= 1 mm.

Skeletonization. — Skeletonization is similar to hole feeding via consumption of the entire thickness of the leaf, but the veins remain intact, often creating a lace-like appearance. The five skeletonization damage types on *C. gettyi* are DT16, DT19, DT22, DT24, DT61 and DT333 (Figure 2.9). DT16 is the most frequently encountered skeletonization damage type and is the nondescript removal of laminar tissue with veins remaining undamaged but lacking a reaction rim of tissue produced by the plant host (Figure 2.9 E). DT19 damage consists of elongate, rectilinear patches of skeletonized tissue with a length-to- width ratio of 2.5 or greater (Figure 2.9 B). DT22 are linear or curvilinear, elongate skeletonized areas parallel to and along the leaf margin (Figure 2.9 A). DT61 is composed of an elongate swath of skeletonization that occurs on one side of a primary or secondary vein (Figure 2.9 D); by contrast, DT24 are three or more circular, skeletonized areas adjacent to a primary or secondary vein (Figure 2.9 C).

Surface Feeding. — Surface feeding is the consumption of one or more layers of surface tissues but not the entire blade thickness and occurs on either the abaxial or adaxial surface of the leaf lamina. The three examples of surface feeding damage types on *Catula gettyi* are DT29, DT30 and DT31, and one previously undescribed damage type of DT333 (Figure 2.10). DT29 is a commonly occurring, circular to polylobate area of surface-feeding damage that is recognizable by the absence of or minimal development of reaction tissue around the perimeter of the feeding zone (Figure 2.10 E). In contrast, DT30 has a well-developed reaction rim with a polylobate margin bordering the surface abrasion patch (Figure 2.10 D), whereas DT31 has a circular bordering margin and also a well-developed reaction rim (Figure

2.10 C). The new surface feeding DT333 consists of polylobate surface abrasions nestled between primary and secondary veins, which leave primary, secondary, and third order venation intact (Figure 2.10 A,B). This damage type is similar to some skeletonization damage types if the fossil leaf counterpart is not preserved; however, inspection of the undamaged side of the laminar tissue clearly reveals that surface feeding is confined to one surface of the leaf.

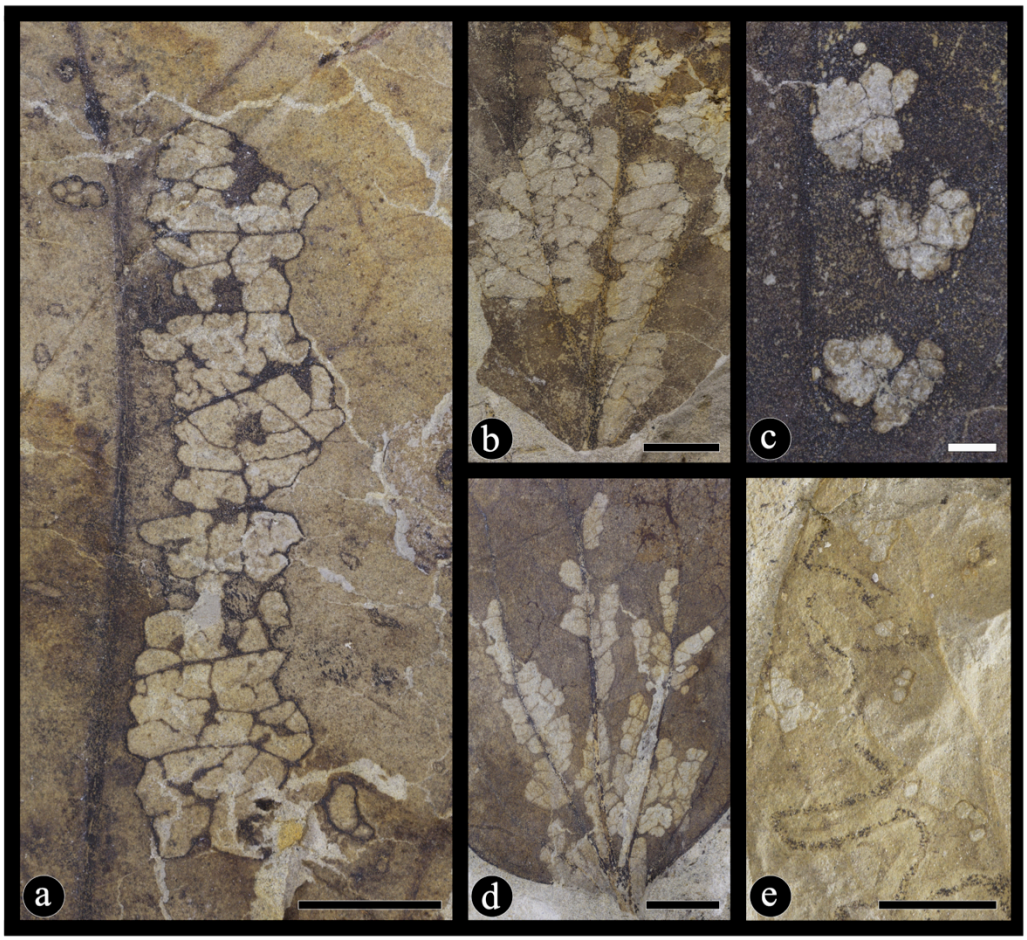


Figure 2.9 (A–E): Skeletonization, the removal of tissue between veins, is represented by five damage types in the *Catula gettyi*: (A) DT22; Skeletonization which follows a primary vein (DMNH 41565); (B) DT19; Broad swaths of skeletonized tissue in a rectilinear shape (DMNH 41568); (C) DT24; Circular areas of skeletonization adjacent to the primary vein (DMNH 41578); (D) DT61; Elongate areas of skeletonization adjoining primary and secondary venation (DMNH 41591); and (E) DT16; Unadorned and common areas of tissue removal between veins (DMNH 41594). Black scale bars= 5 mm; white scale bars= 1 mm.

Figure 2.10 (A–E): Surface feeding on *Catula gettyi* at the Lost Valley Locality consists of three previously known damage types and one new damage type: (A,B) DT333 (DMNH 39725); This new damage type (DT) entails large areas of herbivory in which one surface of the leaf is removed and third-fourth order venation is left intact. Part A exhibits the rank of undamaged venation and does not have surface tissue removed. Counterpart B illustrates the tissue removal and the presence of intact third and fourth order veins. The other three surface feeding damage types are: (C) DT31; Removal of surface tissue with a distinct circular to ellipsoidal reactions rim (DMNH 41589); (D) DT30; Surface feeding with a polylobate reaction rim (DMNH 41566); and (E) DT29; Surface feeding with a weak reaction rim (DMNH 41593). Black scale bars= 5 mm; white scale bars= 1 mm.

Piercing and Sucking. — Piercing-and-sucking insects puncture and suck foliar tissues, such as epidermis, mesophyll, phloem, and xylem. This fluid feeding is accomplished by use of mouthpart elements modified into elongate stylets, often encompassed by an external sheath. There are four piercing and sucking damage types on *C. gettyi*, including the two previously described damage types of DT46 and DT47, and the two recently described damage types of DT219 and DT330 (Figure 2.11). The most common piercing and sucking damage was DT46 (Figure 2.11 B). This damage type consists of one to several concave punctures with an approximate random distribution. DT47 includes many convex punctures that are irregularly distributed along and between secondary veins (Figure 2.11 C). A newly described DT330 consists of a large number (> 50) of punctures covering a substantial portion of the lamina, frequently blanketing smaller areas in a dense sheet (Figure 2.11 D). These punctures occur along, veins of all ranks from primary to tertiary as well as vein inter-areas. These punctures differ from oil glands in that they are more irregular in size and shape and have a highly patchy distribution on the leaf surface.

The enigmatic DT219 is a distinct piercing-and-sucking pattern that consists of two parallel, mirrored lines of punctures indicating a directionality to movement as the putative insect moved across the lamina surface (Figure 2.11 A). Although the identity of this insect herbivore remains unknown, it is possible that this feeding damage represents a sap feeder with mandibulate mouthparts. Because the punctures are paired and evenly spaced, they could be the result of paired mandibles puncturing the leaf surface, followed by ingestion of leaf exudate. Descriptions of this damage

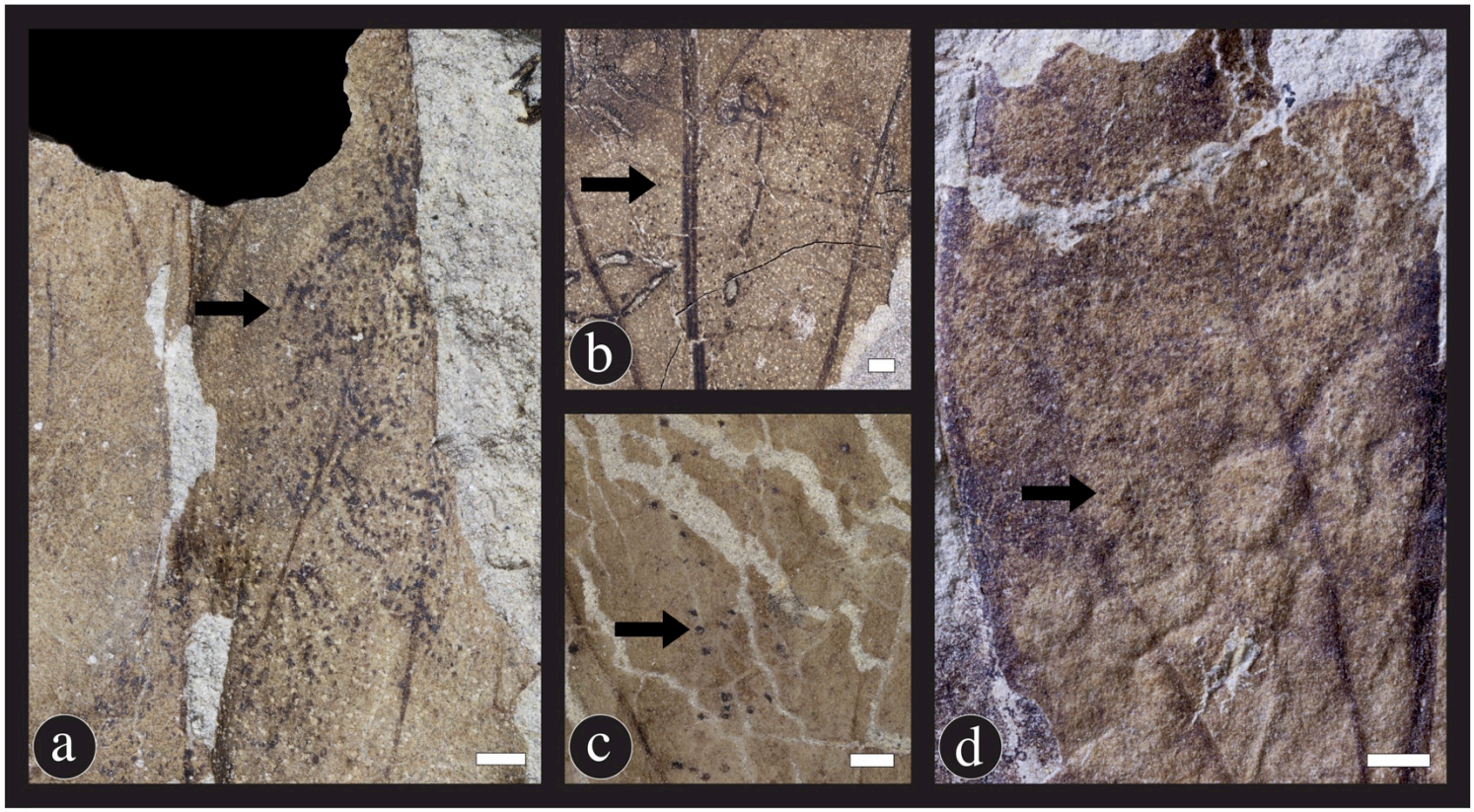


Figure 2.11 (A–D): Insect damage caused by piercing-and-sucking insects. (A) DT219; This damage type (DT) consists of two mirrored lines of puncture marks, which are potentially made by mandibles (DMNH 39724). Additional evidence of piercing-and-sucking insects comes from circular, concave puncture marks DT46 (B) (DMNH 41590); and circular, convex puncture marks DT47 (C) (DMNH 41588). A second new piercing and sucking damage type (D) involves many puncture marks across large portions or the entirety of the leaf lamina (DT330) (DMNH 41569). Scale bars= 1 mm; arrows indicate a single puncture for clarity.

type were figured in two previous studies and redescribed herein. The first description of this unique damage type was from the Late Cretaceous of Israel (Krassilov 2007), which was incorrectly diagnosed as a possible agromyzid leaf-mine damage. We find no evidence of leaf mining for DT219. This type of damage was subsequently identified as surface feeding and described as paired mandibulate "chew marks" of *Araciphyllites tertiaries*, a monocot from the middle Eocene Messel Formation (Wappler et al. 2012). We agree with this latter description, but have reassigned this DT219 to the piercing-and-sucking functional feeding group.

Oviposition. — Oviposition is the deposition of eggs into plant tissue, accomplished by a slicing or piercing insect ovipositor. Oviposition lesions are uncommon on *C. gettyi* leaves. There is one oviposition damage mode, DT101, with only three occurrences of all examined *C. gettyi* specimens (Figure 2.12 D). All three occurrences are represented by one to four oval lesions, replete with robust reaction rims.

Mining. — The most notable and distinctive insect damage type exhibited on *C. gettyi* are leaf mines, which are produced by several lepidopteran (moth) miners (Figure 2.13). There are three types of blotch mines, DT35, DT36 and DT37 (Figure 2.13 F–H), and the two serpentine mines of DT45 and DT332 on *C. gettyi* (Figure 2.13 A–E). The new leaf-mine DT332 is exceptionally abundant on this taxon, occurring on 112 leaf specimens, despite being previously unknown in the fossil record (Figure 2.14). The oviposition site for DT332 mines generally occurs along the leaf margin, and up to seven individual mines may occur on the same leaf specimen. The mines range from 1.4 to 7.1 mm at the broadest width of their mine trajectory.

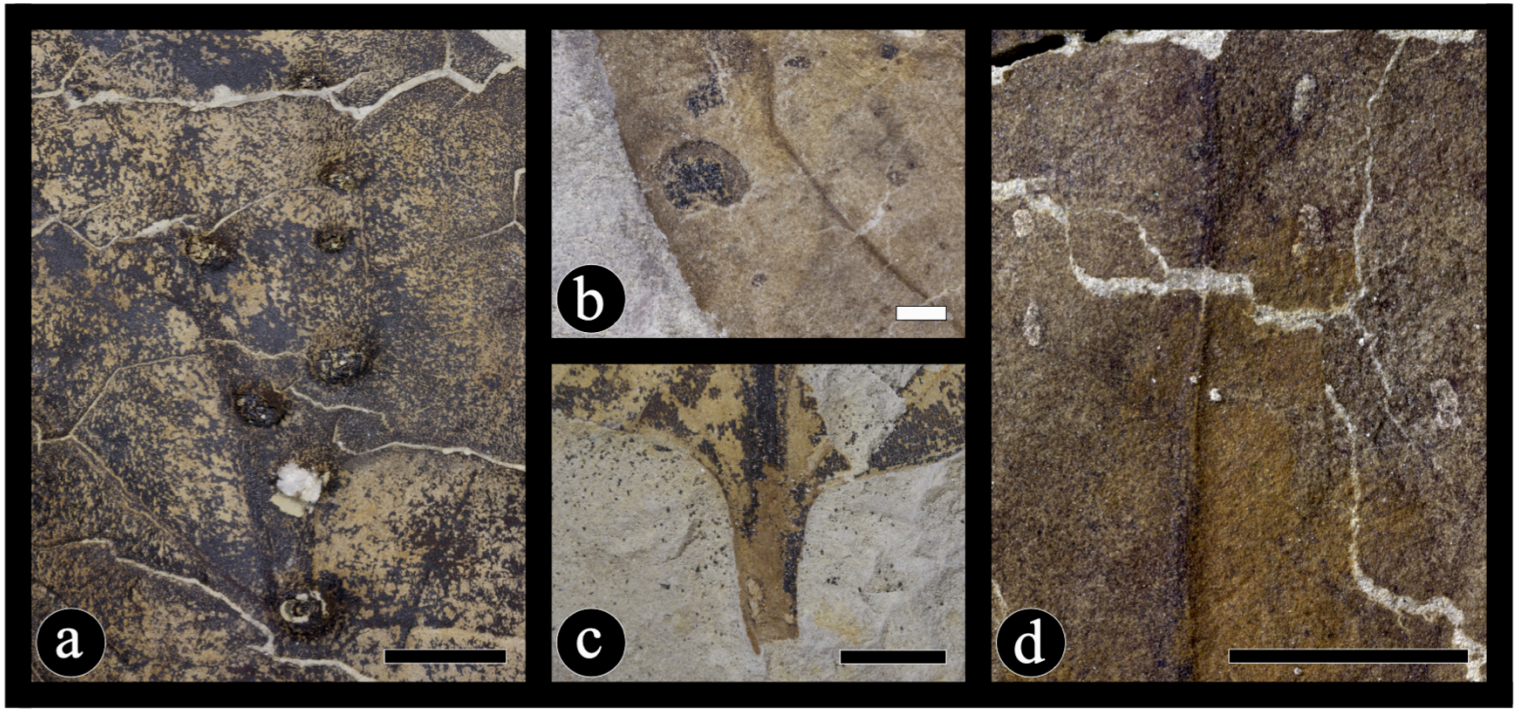


Figure 2.12 (A–D): Galling and oviposition damage on *Catula gettyi*. (A) DT33 & DT34; Galls located on primary veins and secondary veins, respectively (DMNH 41577). (B) DT32; Galls located on the laminar surface, but avoiding primary and secondary venation (DMNH 41573). (C) DT85; Galls located on the petioles of leaves or petiolules of leaves (DMNH 41592). (D) DT101; Oviposition consists of multiple, scattered ovate-shaped scars produced by an insect bearing a robust ovipositor (DMNH 41570). Black scale bars= 5 mm; white scale bars= 1 mm.

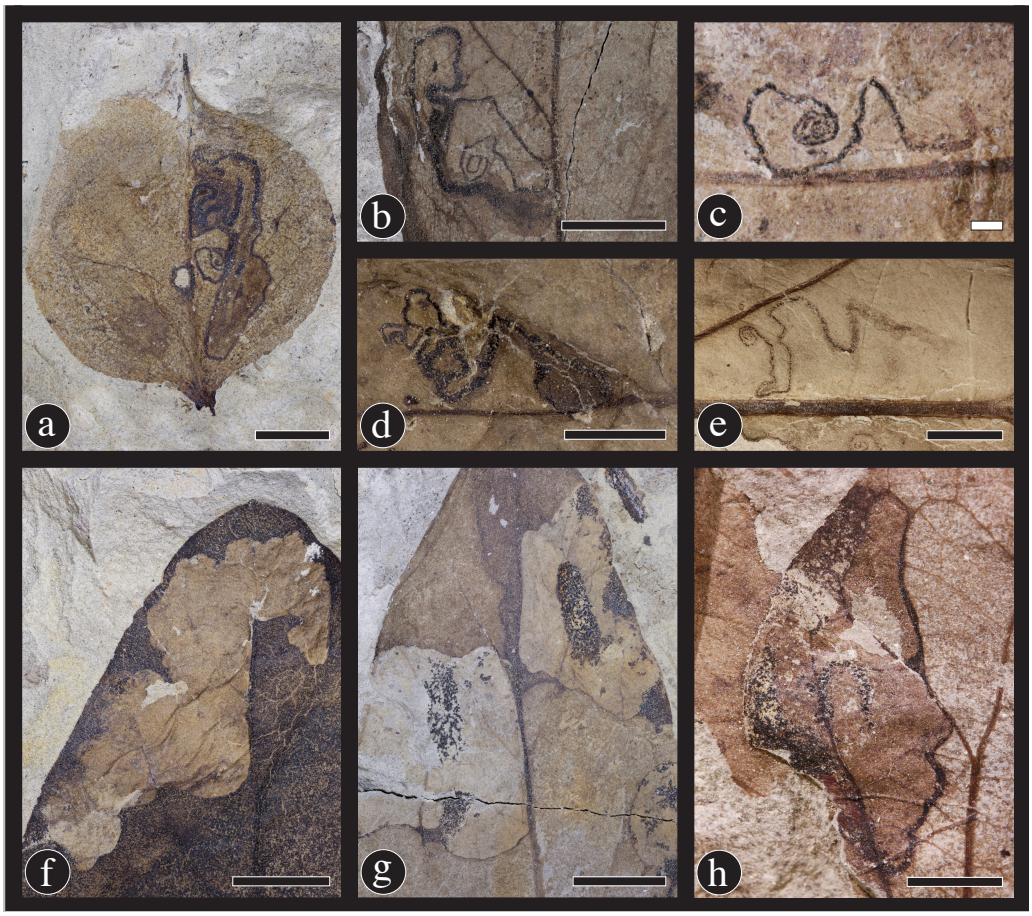


Figure 2.13 (A–H): Leaf mining insect damage at the Lost Valley Locality, Kaiparowits Formation, Utah. (A–E) DT45; Leaf mines attributed to the lepidopteran family Gracillariidae. These five mines illustrate the variation in overall shape, projection, and length, potentially due to the number of instars completed during the mining life history stage (A: DMNH 39732; B: DMNH 41582; C: DMNH 39735; D: DMNH 47124; E: DMNH 39733). The three types of blotch mines include: (F) DT36; A blotch mine lacking internal frass and a central chamber (DMNH 41572); (G) DT35; A blotch mine with frass present in circular central chamber (DMNH 41581); and (H) DT37; A blotch mine with an internal serpentine phase (DMNH 39734). Black scale bars= 5 mm; white scale bars= 1 mm.

The earlier instars produce a minuscule, broadly serpentine shaped mine (Figure 2.14 H–J), while later instars produce a tightly sinuous, intestiniform pattern that often becomes blotch-shaped (Figure 2.14 A–G). Although the insect culprit is unknown, an analogous mine morphology currently appears on several plant hosts today, such as the leaf miners in the genera *Bucculatrix* Zeller 1839 (Lyonettidae) (Opler 1982),

which are similar in size, trajectory, and position compared to DT332 on *C. gettyi*. Based on overall similarities to modern leaf mining moths, including mine size, non-overlapping mine trajectories and presence of solid frass, we posit that DT332 was created by a microlepidopteran leaf miner such as *Bucculatrix* or a related form (Hering 2013, Winkler et al. 2010).

The second, most common leaf-mine is DT45, with 122 specimens on *C. gettyi*, exhibiting one to four mines per leaf (Figure 2.13 A–E). This mine is attributed to the lepidopteran leaf mining family Gracillariidae and was first described by Labandeira and colleagues (Labandeira et al. 2002a, Labandeira et al. 2007c) on specimens of the lauraceous *Marmarthia pearsonii* from the late Maastrichtian Hell Creek Formation (66 Ma) of the Williston Basin in North Dakota, USA. The DT45 mine on *C. gettyi* has a characteristic oviposition site and is initially thread-like and highly coiled, then is succeeded by repeated curvilinear phases, and ends in a sub-rectilinear to ovoidal terminal chamber. Frass is packed and is deployed continuously throughout the serpentine phases of the mine trajectory, with thick, modified bordering tissue constituting roughly 25% of the mine width on both sides of the frass trail. This mine generally is confined between primary and secondary veins, although this feature is variable on smaller leaves. DT45 varies substantially in size and length, which may be attributed to conspecific aborted mines and behavioral differences in larval instar activities.

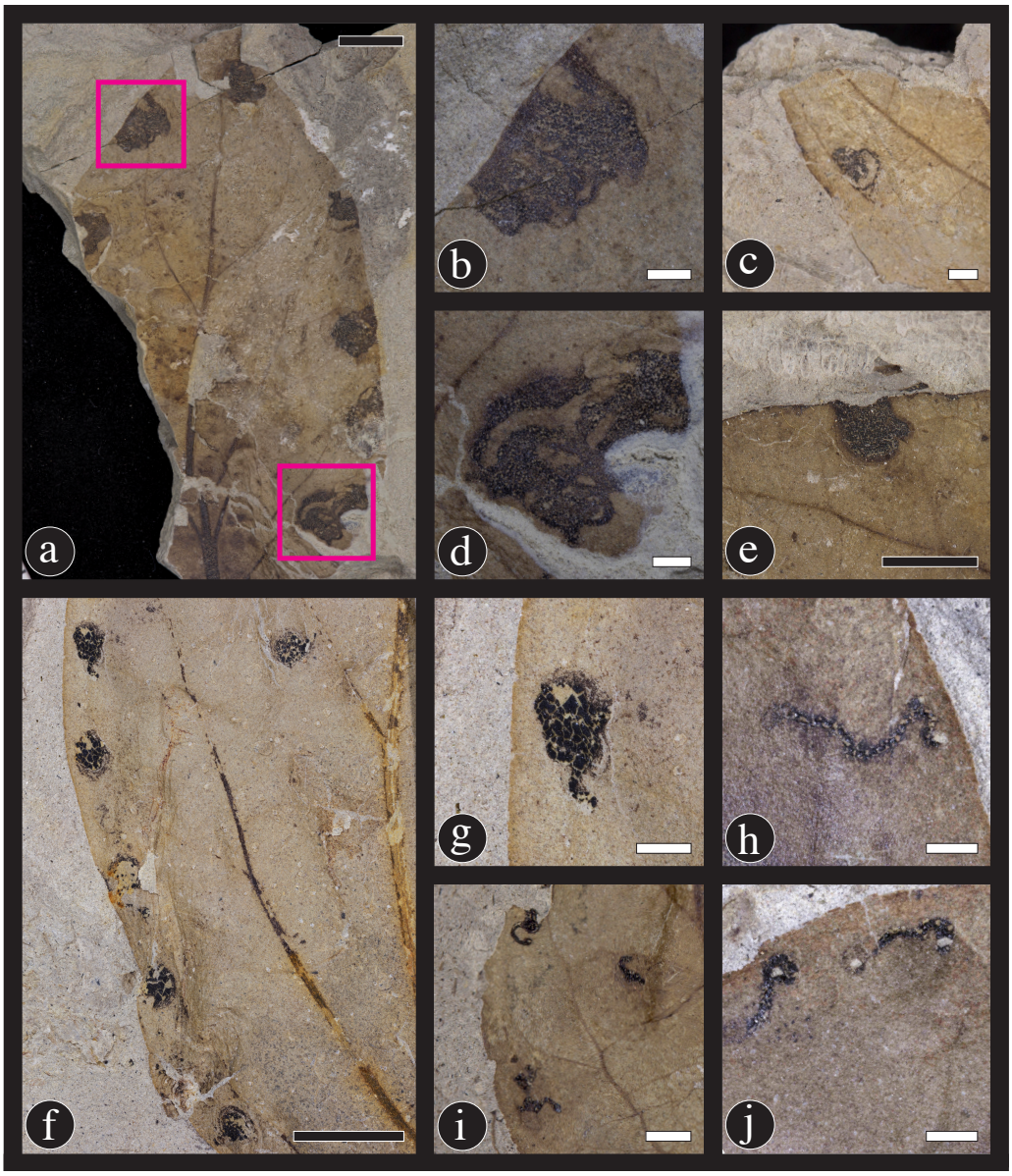


Figure 2.14. (A–J): New leaf mine damage type on *Catula gettyi*. DT332 includes a range of leaf mine shapes, including (A) roughly circular mines with serpentine trajectories visible within the mine (DMNH 39726), close up of mines outlined (B, D); (E) leaf mines with a circular chamber and no evident serpentine trails (DMNH 41587); (C) a linear phase followed by a solid, circular chamber (DMNH 47126), (F) (DMNH 39737), close up of mine outlined (G,I) (DMNH 41597); and (H) (DMNH 41597), (J) (DMNH 41597) mines with linear trajectories. Differences in mine form are likely attributable to the number of instars completed by each individual. These mines are typically found along the margin of *C. gettyi* leaves. Black scale bars= 5 mm; white scale bars= 1 mm.

Three blotch-mine damage types are found on *C. gettyi* leaves in the Lost Valley Locality. DT36 is the most frequently encountered of the blotch mine damage types (Figure 2.13 F). The DT36 mine consists of variously shaped compartments that lack a central chamber and sometimes contain spheroidal fecal pellets among the frass (Labandeira et al. 2007c). A similar mine is DT35, a blotch mine with a central chamber present, also commonly associated with spheroidal frass (Figure 2.13 G). The third blotch mine, DT37, consists of a polylobate shaped blotch with an internal serpentine stage (Figure 2.13 H).

Galling. — Galls are envelopes of plant tissue that are induced and inhabited by insects, mites, nematodes, fungi, or bacteria. Insect galls generally consist of a hardened outer wall for protection and an inner layer of softer nutritive tissue connected to the host-plant organ by vascular tissue, all of which encapsulate an innermost chamber or chambers (Meyer 1987). The four gall damage types on *C. gettyi* are located on the leaf lamina, consisting of nondescript DT32, DT33 and DT34, and the petiole gall DT85 (Figure 2.12). DT32 consists of circular to ellipsoidal galls occurring on the leaf lamina and avoidance of major veins (Figure 2.12 B). DT33 and DT34 represent galls similar in form to DT32, but instead occur on secondary veins and primary veins, respectively (Figure 2.12 A). The distinctive DT85 is small, lenticular to ellipsoidal gall situated lengthwise along a midrib or petiole, with indistinct inner nutritive tissue and a thick, dark outer wall located on the petiole of *C. gettyi* (Figure 2.12 C).

Insect Herbivory on Late Cretaceous Laurels

The four Maastrichtian-aged laurel taxa (*Marmarthia pearsonii*, *M. trivialis*, *"Artocarpus" lessigiana*, and "*Ficus" planicostata*) and the Campanian-aged *Catula gettyi* had comparatively similar damage-type richnesses (Figure 2.15). The 95% confidence intervals of all five taxa overlapped in the rarefaction analysis for damage-type richness by total surface area. Intensities of insect herbivory, i.e. herbivory index, were also relatively similar among four of the five taxa (Table 2.2; Figure 2.16). Herbivory indices ranged between 2.86% and 0.37%, with 95% confidence intervals overlapping for all taxa except *"A." lessigiana*, which has a lower herbivory index than *C. gettyi* and *M. trivialis* (Figure 2.16).

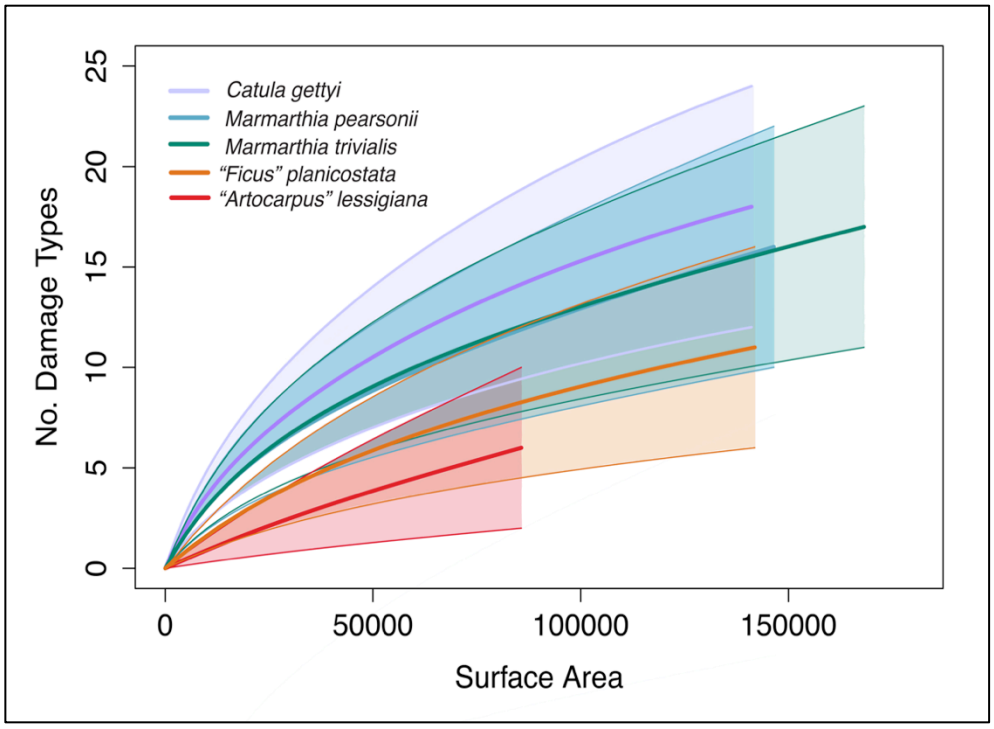


Figure 2.15: Rarefaction of damage types and total sampled surface area for *Catula gettyi* and the four Hell Creek taxa (*Marmarthia pearsonii*, *M. trivialis*, "*Artocarpus*" *lessigiana*, and "*Ficus*" *planicostata*).

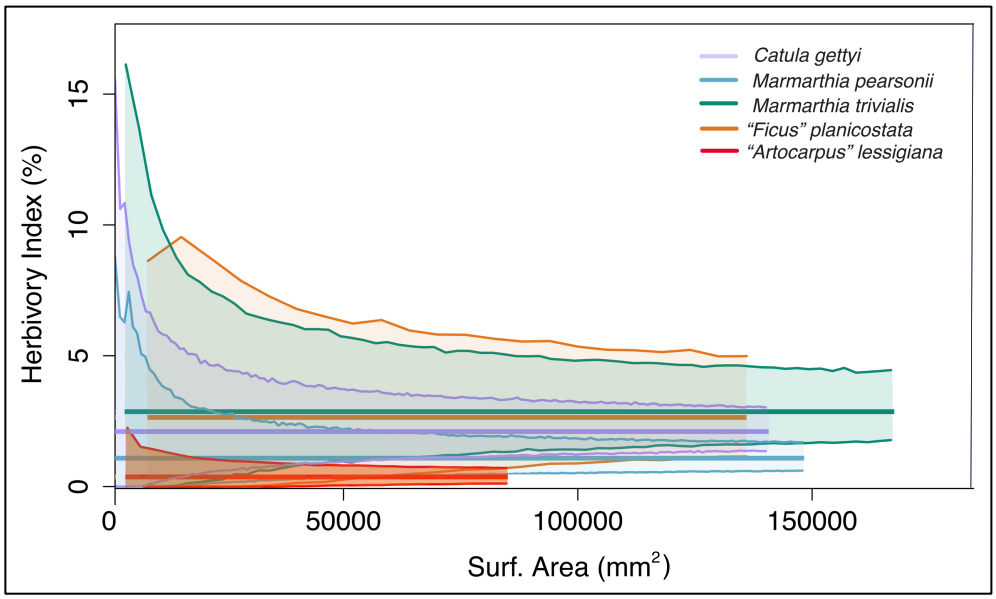


Figure 2.16: Herbivory indices of four Hell Creek taxa ("*Ficus*" *planicostata*, *Marmarthia trivialis*, *M. pearsonii*, and "*Artocarpus*" *lessigiana*) and *Catula gettyi*. Confidence intervals are set at 95%.

Table 2.2: Comparisons of herbivory between Late Cretaceous taxa in the family Lauraceae: *Catula gettyi* (Kaiparowits Formation, 75.6 Ma), and the Hell Creek taxa (66.5 Ma) *Marmarthia pearsonii* (Loc. 428), *M. trivialis* (Loc. 900), "*Artocarpus*" *lessigiana* (Loc. 428), and "*Ficus*" *planicostata* (Loc. 428) (Labandeira et al. 2002a).

	Catula gettyi*	***Marmarthia trivialis***	***Marmarthia pearsonii***	***"Artocarpus" lessigiana***	***"Ficus" planicostata***
Number of specimens analyzed for surface area	156	67	167	32	23
Proportion of specimens with herbivory	40.76%	47.76%	20.40%	21.88%	60.87%
Total surface area (mm^2)	142036.327	170748.468	147371.987	88484.531	148379.603
Herbivorized surface area (mm^2)	2985.841	4886.361	1598.448	325.244	3921.650
Herbivory index	2.102%	2.862%	1.085%	0.368%	2.643%
Number of damage types	19	17	17	6	11

Finally, the spectrum of insect herbivory differed among the five laurel taxa (Figures 2.17, 2.18). The nonmetric multidimensional scaling (NMDS) ordination plot that was subsampled to 85,000 mm^2, which included all five taxa, illustrated a great deal of overlap between *C. gettyi* and *M. pearsonii* (Figure 2.17). Moreover, both *C. gettyi* and *M. pearsonii* were strongly associated with endophytic feeding groups of leaf mining and oviposition, as well as piercing and sucking.

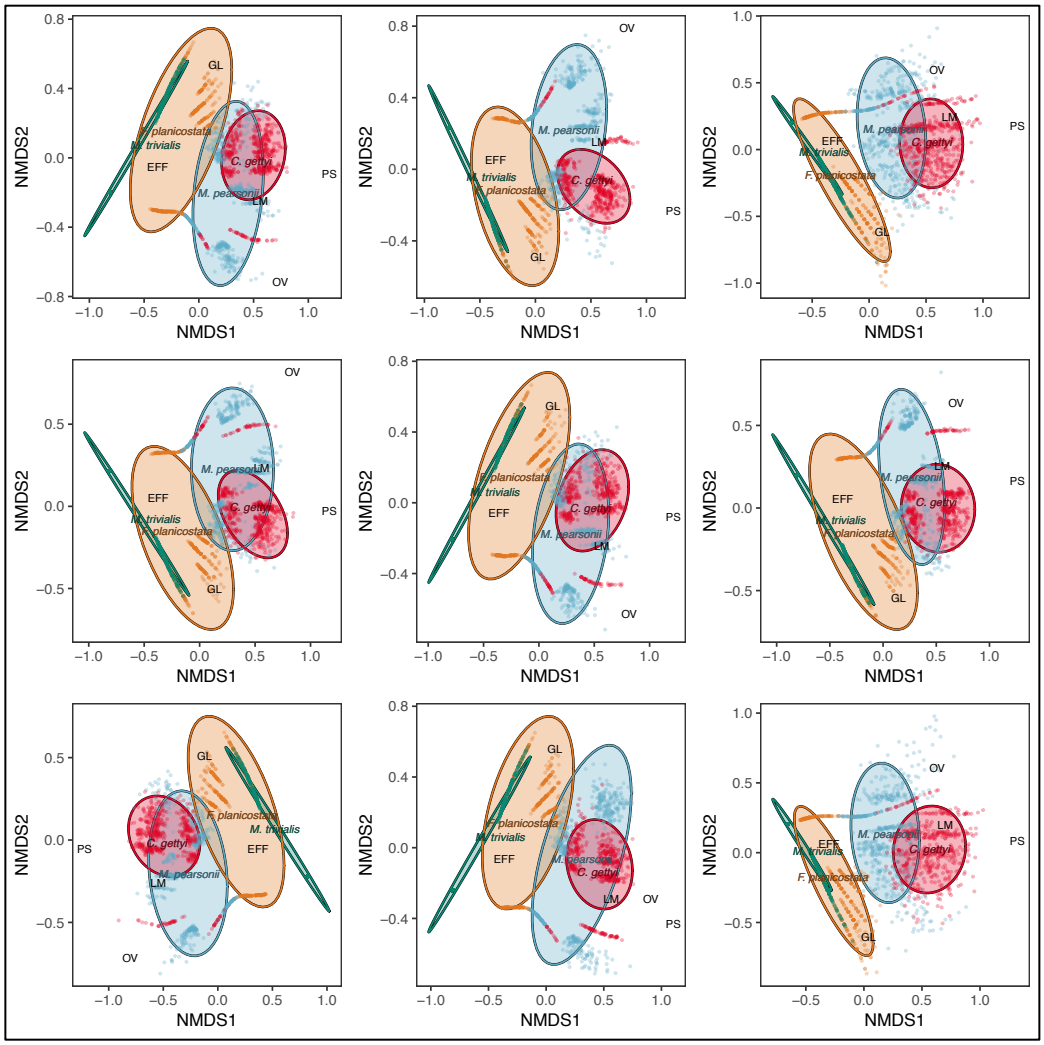


Figure 2.17: Non-metric multidimensional scaling (NMDS) ordination subsampled at 85,000 mm^2 with elipses, which include 84% of the datapoints closest to the centroid, for . *Catula gettyi* and the four Hell Creek taxa (*Marmarthia pearsonii*, *M. trivialis*, "*Artocarpus*" *lessigiana*, and "*Ficus*" *planicostata*).

Marmarthia trivialis, "*F.*" *planicostata*, and *"A." lessigiana* were tightly clustered in morphospace and associated with external functional feeding groups and gall makers. These patterns were more pronounced in the NMDS ordination plot that subsampled 140,000mm^2, which clearly shows the overlap in morphospace between *C. gettyi* and *M. pearsonii*, and their shared association of leaf mining (Figure 2.18).

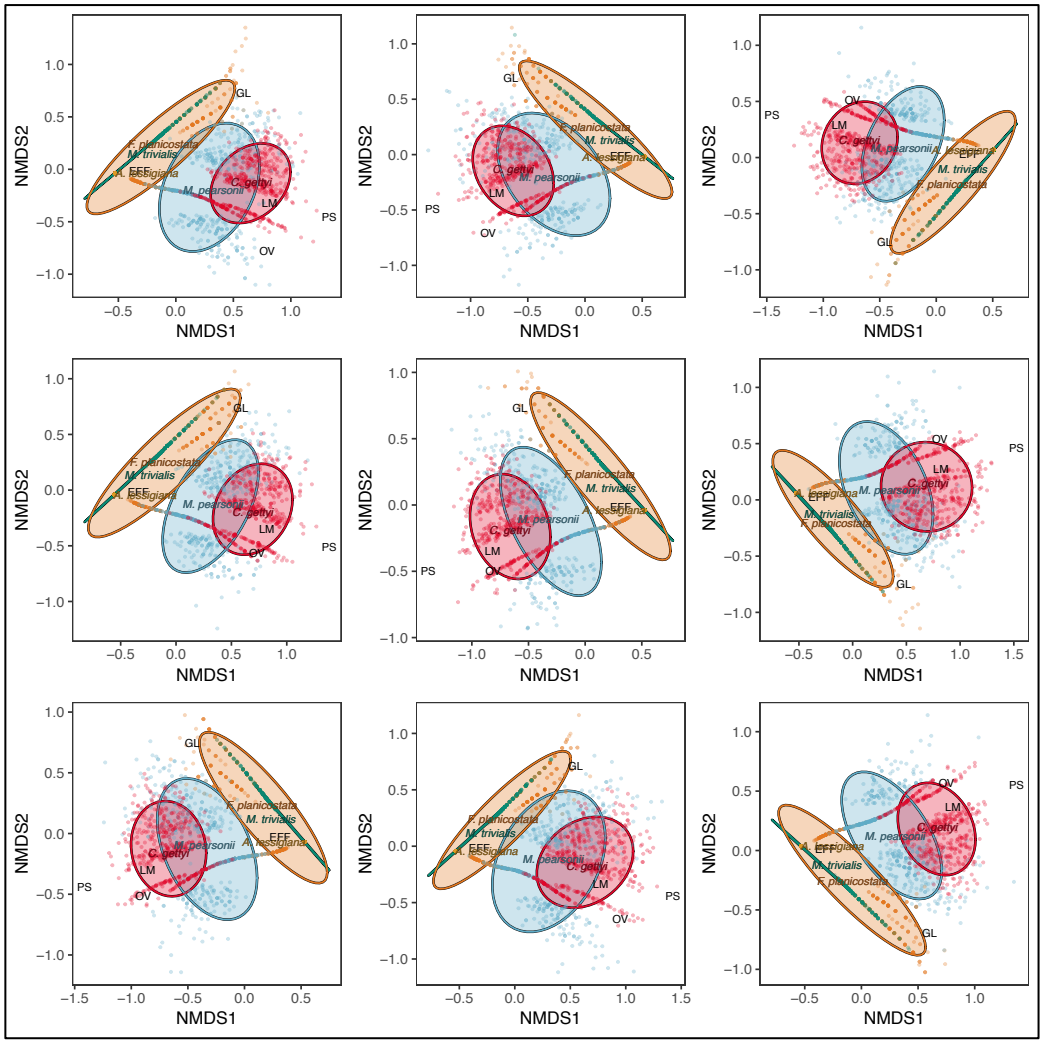


Figure 2.18: Non-metric multidimensional scaling (NMDS) ordination subsampled at 140,000 mm^2 with elipses, which include 84% of the datapoints closest to the centroid, for *Catula gettyi* and three Hell Creek taxa (*Marmarthia pearsonii*, *M. trivialis*, and "*Ficus*" *planicostata*).

Discussion

The damage intensity and richness of insect damage on fossil leaves of *Catula gettyi* from the Kaiparowits Formation, combined with that of the latest Cretaceous Hell Creek Formation (Labandeira et al. 2002a, Labandeira et al. 2002b), provide a baseline to better understand Late Cretaceous herbivorous insect fauna and their associations with plants. Below, we discuss overall patterns of Kaiparowits insect herbivory, compare these results to other Late Cretaceous taxa, and consider the impact of sampling effort and damage-type richness for insect herbivores in the Late Cretaceous fossil record.

Kaiparowits Formation Insect Richness

The plant–insect associations of the Kaiparowits Formation are both diverse and abundant on *Catula gettyi* leaves. We found evidence for eight functional feeding groups, 40 damage types, 863 occurrences of insect damage, an herbivory index of 2.102%, and 38.1% of *C. gettyi* leaves exhibiting insect herbivory. Interestingly, there are an elevated number of scale insect species on particular host species of extant Lauraceae (Foldi and Watson 2001, Green 1917, Hutton 1997, Miller and Davidson 2005), although no scale insects were found on *C. gettyi*. By contrast, the frequency of leaf miners on modern Lauraceae are minimal (Spencer 2012), yet diverse and abundant on *C. gettyi*. In general, the spectrum of insect damage on *Catula gettyi* is similar to that found on modern laurels (for a discussion on modern Lauraceae herbivory, see the Supplementary Material in Appendix B). The external foliage feeding damage types of hole, margin and surface feeders as well as skeletonizers, are

at typical levels of richness expected for a moderately diverse host-plant family such as Lauraceae.

The distribution of host specificity was nearly evenly divided among damage types, wherein specialized (12 total), intermediate (15 total), and generalist (13 total) damage types each accounted for approximately one third of the total number of damage types. Nevertheless, the distribution of host specificity for individual occurrences was bimodal, with greater generalist and specialist insect damage. Approximately half of all damage-type occurrences were assigned to the generalist category (51.9%), a small number were intermediate (8.8%), and specialist damage was also relatively high (39.3%). For qualitative categories, hole feeding (198 instances) and margin feeding (214 instances) had the most occurrences of generalist damage. Specialist damage was closely associated with endophytic feeding modes, most notable of which were the five leaf mining damage types constituting 311 occurrences, likely dominantly monophagous in host specificity. The combination of high damage-type richness – including many distinct specialist damage types – suggests that *C. gettyi* likely hosted a high richness of insect herbivores.

In modern communities, endophytic insects most often make one, characteristic damage type on a single plant-host species (Bairstow et al. 2010, Carvalho et al. 2014, Currano et al. 2008, Wilf and Labandeira 1999). This is because feeding behavior often is highly constrained and can sometimes be attributed to a taxonomic level of the subfamily, especially for endophytic feeders such as scale insects, leaf miners, and gallers (Jud and Sohn 2016, Labandeira et al. 2007c, Wilf et al. 2000). Alternatively, ectophytic (chewing) insects are more likely to consume a

wider range of host-plant species and often produce more numerous and diverse damage on leaves than their endophytic counterparts, which makes estimating ectophytic insect richness difficult in the fossil record (Carvalho et al. 2014). Furthermore, a particular generalist damage type may be produced by multiple species of insects and, alternatively, one species of insect may be capable of producing several damage types. While we do not hypothesize an exact number of insect herbivores on *Catula gettyi*, we estimate that the specialized insect damage provides evidence for at least 12 specialist insect herbivores from the 40 total damage types. For comparison, the number of arthropod herbivores on a single host-plant species in modern ecosystems varies greatly, with up to 205 phytophage species on leaves of certain taxa (e.g. Basset and Novotny 1999, Kennedy and Southwood 1984, Novotny et al. 2002b, Novotny et al. 2006). Our survey of *C. gettyi* captures many fewer herbivores. However, we are not able to measure fossil plant–insect associations with the same accuracy as modern plant–insect associations. As a result, the observation of 40 damage types on a single fossil taxon is among the highest of any known fossil taxon (e.g. Adroit et al. 2018b, Möller et al. 2017, Wappler et al. 2012).

Antiherbivore Resistance and Herbivore Specialization

Modern Lauraceae produce significant levels of secondary compounds and structural defenses. Many species of Lauraceae are noted for their elevated concentrations of essential oils that typically are employed in defenses against a wide range of insect herbivores today (González-Coloma et al. 1994a, González-Coloma et al. 1994b). For example, lauraceous foliage is known to be rich in monoterpenes

(Goralka and Langenheim 1996, Niogret et al. 2013); sesquiterpenes (Niogret et al. 2013); phenols of vanillic, chlorogenic, *p*-coumaric and ferulic acids (Ingersoll et al. 2010); as well as cyanoid diterpenes, extracts of cyandol, cyanoids and cinnceylanol (González-Coloma et al. 1994b). These are known to have negative effects when fed to insects; the physiological outcomes of these extracts range from subtle antifeedent effects to toxins causing death (González-Coloma et al. 1994a). Growth inhibition also is known for several lepidopteran (moth), coleopteran (beetle), and blattodean (termite) herbivores (González-Coloma et al. 1994b, Kishimoto-Yamada et al. 2013). In addition to chemical defenses, Lauraceae possess considerable structural defenses. Features frequently found in Lauraceae indicating mechanical impediments to insect herbivory principally involve leaf toughness, such as thickened epidermis layers, cell-wall rigidity, thick cuticle, and robust fiber strands (Grubb 1986). As with the majority of modern Lauraceae, a combination of structural and chemical defenses was likely present in *C. gettyi* (also see Supplementary Materials in Appendix B).

Although antiherbivore defenses in *Catula gettyi* can only be inferred, the morphology of the leaves suggest tough, long-lived leaves, similar to many extant Lauraceae species (Bentley 1979). The leaves of *C. gettyi* have relatively thick petioles compared to their leaf area suggesting a high leaf mass per area quotient, though this analysis is pending. Furthermore, they show generally less physical damage, such as blade tearing and necrotic tissue, compared to other leaf morphotypes at the Lost Valley locality. The antiherbivore defenses of long-lived leaves generally are constitutive (ever-present) whereas the metabolites are typically qualitative defenses, such as digestibility-reducers that are present at high levels

(Coley 1988, Karban and Baldwin 2007), and are known to decrease the probability of insect herbivory from a wide range of both generalist and specialist insect herbivores (Feeny 1976, Rhoades and Cates 1976). Furthermore, long-lived leaves typically have lower photosynthetic rates and lower nitrogen content and greater structural tissues, which makes them less nutritious and palatable to insects (Coley et al. 1985). The morphology of the leaves and the bimodal distribution of generalist and specialist damage types on *C. gettyi* are indicative of a plant species with constitutive defenses, such as the structural defenses that slow or prevent processing of leaf material by insect herbivores.

At present, secondary metabolites are poorly known in fossil leaves though efforts to detect and identify them are increasing (Labandeira et al. 2014, McCoy et al. in press). Nevertheless, specialized insect damage types can be used, such as those made by leaf miners, to provide predictions about the role of secondary metabolites in *Catula gettyi*. A longstanding hypothesis is that elevated secondary compound defenses in plants often lead to taxon-specific coevolutionary relationships between the plant host and insect herbivore (Ali and Agrawal 2012). Specialist insects frequently have physical adaptions to their host plant's secondary compounds, particularly involving tolerance, expulsion, or sequestration, although it is acknowledged that specialist herbivores also are negatively impacted by these toxins at high levels (Cornell and Hawkins 2003). Moreover, insects instead use one or more particular toxic compounds as a cue to recognize potential plant hosts as edible or suitable as an oviposition site (Rosenthal and Berenbaum 2012, Tallamy 1986).

Catula gettyi hosts both abundant and diverse, specialized damage types, such as piercing and sucking, galling, and most notably leaf mining. The elevated number of leaf-mine occurrences is exceptional in the fossil record compared to other plant host species (ex. Arens and Gleason 2016, Donovan et al. 2018, Donovan et al. 2014, Krassilov 2007, Krassilov and Shuklina 2008, Krassilov 2008a, Labandeira et al. 1994, Labandeira et al. 2002a, Labandeira et al. 2002b); 7.8% of *C. gettyi* specimens have the leaf mine DT45 and 7.2% have DT332, which are both attributed to lepidopteran miners. Lepidopteran leaf miners are well known for their abilities to disarm, digest, and/or tolerate plant secondary metabolites as an ever-present threat while living inside the leaf mesophyll (Nishida 2002). The exceptionally high number of these two damage-type occurrences, the specialist nature of these leaf mines, and the lack of these mines on other plant taxa from the same locality indicates that two leaf mining lepidopteran taxa were actively seeking out *C. gettyi* as an oviposition site for their larvae.

Late Cretaceous Insect Herbivory

Insect herbivory studies in the Mesozoic are lacking relative to those of the late Paleozoic and Cenozoic (Pinheiro et al. 2016), with only a small number of Late Cretaceous floras having been analyzed for insect herbivory (Labandeira 2006b). Among these studies, there are only a handful of descriptions for isolated Mesozoic damage types (ex. Cenci and Adami-Rodrigues 2017, Jud and Sohn 2016, Krassilov 2007, Krassilov 2008a, Labandeira 1998c, Labandeira et al. 1994, Stephenson 1992, Vasilenko 2008, Wilf et al. 2000) and two, fully described, insect damaged floras from the Late Cretaceous that predate the Kaiparowits Formation (Table 2.3). Of the

two floras for which the damage has been fully described, the Soap Wash Formation of Utah (98.1 Ma) has an admittedly small sample size (152 specimens) (Arens and Gleason 2016), and the Ora Formation Flora of Israel (91 Ma) (Krassilov and Shuklina 2008) does not use the damage type scheme (Labandeira et al. 2007c). The lack of damage type designations, small sample sizes, and the approximation of specimen numbers and herbivory occurrences precludes a direct comparison of the Ora and Soap Wash formations to the Kaiparowits Formation regarding insect herbivory. Aside from these Late Cretaceous deposits, only the Late Maastrichtian Hell Creek Formation in North America and the Lefipán Formation in South America, both of which are ca. 8–10 million years younger than the Kaiparowits Formation, provide a comparable Late Cretaceous dataset of insect herbivory.

The Hell Creek and Lefipán formation studies (Table 2.3) have yielded relatively high damage-type richness, between 32 and 60 damage types (Donovan et al. 2016, Donovan et al. 2014, Krassilov 2007, Labandeira et al. 2002a, Labandeira et al. 2002b, Wappler et al. 2009, Wilf et al. 2006). However, differences in habitat type, sampling intensity, sampling protocol, floral diversity, time averaging, deposit size, taphonomic variability, number of localities, and latitudinal position make comparisons among floras inequitable. Although comparisons between the Kaiparowits Formation insect herbivory and the insect herbivory in these floras are inadvisable for these reasons, individual taxa from the Maastrichtian of North America collected from a single locality are analogous to the sampling of *C. gettyi* and therefore permit a more appropriate comparison. Given this context, we selected all taxa belonging to the family Lauraceae that had at least 20 specimens from a

Table 2.3. Late Cretaceous floras analyzed for herbivory.

Formation	**State, Country**	**Age (Ma)**	**Number of Plant Taxa**	**Number of Specimens**	**Herbivorized Specimens**	**Number of DTs**	**References**
Soap Wash	Utah, USA	98.4	18	152	64	19	Arens and Gleason (2016)
Ora	Negev, Israel	~91	~50	~1500	N/A	~60*	Krassilov and Shuklina (2008)
Kaiparowits	Utah, USA	~75.6	1	1564	606	40	*This study*
Hell Creek	North Dakota, USA	67-66	191	4149	657	32	Labandeira et al. (2002a,b)
Lefipán	Patagonia, Argentina	67-66	53	856	533	50	Donovan et al. (2016, 2018)

*Does not use damage type classification from Labandeira et al. (2007)

single locality in the Hell Creek Formation (Johnson 2002), which between the two terminal Cretaceous studies is geographically closest to the Kaiparowits Formation. Four lauraceous taxa from the Hell Creek Formation met these requirements: *Marmarthia pearsonii* (HC162, Locality 900), *Marmarthia trivialis* (HC105, Locality 428), "*Artocarpus*" *lessigiana* (HC179, Locality 428), and "*Ficus*" *planicostata* (HC4, Locality 428) (Table 2.3) (Supplementary Figure 2.2).

Catula gettyi has similar richness of damage types when compared to *Marmarthia pearsonii, M. trivialis, "Artocarpus" lessigiana,* and *"Ficus" planicostata* (Figure 2.15). Although *C. gettyi* has a high number of damage types across all 1,564 specimens, rarefaction analysis of damage-type richness by surface areas illustrates that the levels of insect damage are comparable to the Hell Creek laurels. Regarding the types of insect damage found on each taxon, *C. gettyi* and *M. pearsonii* are most tightly associated with leaf miners. Notably, the specialist leaf mine DT45 only occurs on *C. gettyi* and *M. pearsonii* among the five lauraceous taxa, perhaps due to similar antiherbivore defenses. It is possible that this leaf miner is well accommodated to the secondary metabolites of some Lauraceae species. DT45 is also present on morphotypes "LEF5" and "LEF9" from the Lefipán Formation, although their taxonomy is currently unresolved (Donovan et al. 2018). Future analyses comparing *C. gettyi* to other Late Cretaceous plants in Lauraceae and other angiosperm lineages should clarify the insect damage associations between these Late Cretaceous plant hosts. Indeed, we advocate for more taxonomic work in Late Cretaceous floras, coupled with ecological data for each plant host. This would particularly be useful for elucidating the forces driving patterns of Late Campanian

regionalism and disparities in taxonomic richness observed in vertebrates (Gates et al. 2012, Loewen et al. 2013, Nydam 2013, Woolley et al. 2020) and invertebrates (Tapanila and Roberts 2013). Latitudinally dispersed floras and associated indicators of insect richness from penecontemporaneous or paracontemporaneous geologic units in the Western Interior are key to understanding how abiotic factors, such as sea level, climate, and tectonics influenced Late Cretaceous ecosystems.

Conclusions

Herein we describe the new genus and species, *Catula gettyi* (Laurales: Lauraceae), from the Campanian Age Kaiparowits Formation of southern Utah, USA and catalog the insect damage on the taxon. With 1,564 studied museum voucher specimens, *C. gettyi* is among the best-sampled Mesozoic taxa in the fossil record for insect damage. Insect herbivory on *C. gettyi* is both rich and abundant, including eight functional feeding groups, 40 damage types, an herbivory index of 2.1, and 38.1% of the specimens exhibiting at least one type of insect damage. There was a large damage component of generalist, ectophytic feeding as well as six specialist leaf miners. These results, in combination with the analysis of four Late Cretaceous lauraceous taxa from the Hell Creek Formation, show similar damage-type richnesses for these Late Cretaceous lauraceous plant hosts and possible specialization on lauraceous plant hosts.

Taken together, this first analysis showing the richness, abundance, and intensity of insect damage on a single taxon in the Kaiparowits Formation, which

complements the high richness seen in vertebrates, invertebrates, and plants known from this geologic formation. Future work will assemble the insect–plant ecosystem and investigate how the base of the food web reflects diversity seen at higher trophic levels, including that of the diverse Kaiparowits Formation dinosaurs.

Acknowledgments

We dedicate this paper to the memory of our dear friend and colleague, Mike Getty. We are grateful to the Denver Museum of Nature & Science's Leaf Whackers for preparation of the Kaiparowits fossil specimens and to K. MacKenzie, G. Rossetto, T. Foreman, N. Toth, N. Neu-Yagle, and R. Rissman for their support. Thanks to R. Wicker for his photographs of the Hell Creek Formation specimens. BLM Cooperative Agreement L14AC00302 and donors to the Denver Museum of Nature & Science Laramidia Project provided financial support for fieldwork. The Denver Museum of Nature & Science provided additional financial support for collections work during the summer and fall of 2017. Thanks to J. Shultz for his mentorship and S. Schachat for her guidance and skills in *R*, which she generously shares with colleagues. We thank the three reviewers and editorial team at *PLoS ONE*. Finally, we thank President Bill Clinton, Secretary of the Interior Bruce Babbitt, and countless public servants for the creation of the Grand Staircase-Escalante National Monument, and all those who fight to protect our national public lands today. This is contribution 372 from the Evolution of Terrestrial Ecosystems consortium at the National Museum of Natural History in Washington, D.C.

Chapter 3: Plant–insect associations of a Kaiparowits Formation locality, Upper Cretaceous of Utah, USA

Abstract

The Upper Cretaceous Kaiparowits Formation (76.49 ± 0.14 to 74.69 ± 0.18 Ma), located primarily within the Grand Staircase-Escalante National Monument of south-central Utah, has a well-documented paleontological record that continues to enhance our understanding of Campanian Age (83.6–72.1 Ma) ecosystems. To date, there are no insect body fossils described from the Kaiparowits Formation and the diversity of herbivorous insects is as yet unknown. However, the abundant evidence of insect herbivory—the chew marks, holes, punctures, galls, and leaf mines in fossil leaves—provides evidence for the intensity and richness of Kaiparowits insect feeding behaviors and mouthpart morphologies. A total of 719 plant specimens comprising angiosperms, lycopsids, pteridophytes, sphenophytes, gymnosperms, and unassociated reproductive organs from the JARS locality were analyzed for signs of insect herbivory. This is the first examination to describe and quantify plant–insect associations for an entire Campanian locality.

Introduction

Paleontologists have studied the fossil fauna and flora of the Campanian Age Kaiparowits Formation (Upper Cretaceous, 76.49 ± 0.14 to 74.69 ± 0.18 Ma) for over

four decades in order to reconstruct these exceptionally diverse ancient ecosystems (Titus and Loewen 2013). This diversity includes non-avian dinosaurs (Carr et al. 2011, Decourten and Russell 1985, Gates and Sampson 2007, Lund et al. 2016, Sampson et al. 2010b, Sampson et al. 2013, Zanno et al. 2013), birds (Farke and Patel 2012), pterosaurs (Farke and Wilridge 2013), squamates (Lively 2015, 2016, Lyson et al. 2017, Nydam 2013), amphibians (Gardner and DeMar 2013, Roček et al. 2013), crocodyliforms (Farke et al. 2014, Irmis et al. 2013), mammals (Cifelli 1990a, b, Eaton and Cifelli 1988, Eaton et al. 1999), fish (Brinkman et al. 2013, Kirkland et al. 2013), aquatic invertebrates (Roberts et al. 2008, Tapanila and Roberts 2013), plants (Maccracken et al. in review-a, Maccracken et al. 2019, Miller et al. 2013), and fossil traces of insect behavior (Maccracken et al. in review-a, Roberts et al. 2007, Roberts and Tapanila 2006). However, insect body fossils from this formation are virtually absent, despite the high probability that insects were the most abundant and diverse group of animals in the Kaiparowits Formation (Labandeira 2006a, Labandeira and Eble 2005). This absence means that, to date, reconstructions of the Kaiparowits ecosystems and food webs are very much incomplete (Titus and Loewen 2013).

Insect body preservation during the Late Cretaceous (100—66 Ma) in the Western Interior of North America is poor (Ross et al. 2000), and is not only restricted to within the Kaiparowits Formation. Insect body fossils from Upper Cretaceous deposits of North America are primarily known from Campanian Age Canadian Amber found in the Foremost Formation (Carpenter et al. 1937, McAlpine and Martin 1969, Pike 1994), and Turonian Age (93.9–89.8 Ma) Raritan Amber of New Jersey, USA (Grimaldi and Agosti 2000, Grimaldi et al. 2010). The general lack

of insect body fossils, especially compression-impression fossils, from the Late Cretaceous may be due to high global sea levels, which flooded large swaths of the North American landmass and greatly reduced the extent of depositional environments conducive to insect fossilization (Gale 2000, Ross et al. 2000, Szwedo and Nel 2015). However, it remains puzzling as to why insect fossils nonetheless are rare in Upper Cretaceous deposits, particularly extensive freshwater habitats that ostensibly could preserve insects. Insect preservation commonly requires rapid burial in anoxic conditions, most often in lakes and ponds (Smith 2012). Water depth, alkalinity, temperature, sediment type, grain size, insect size, and insect morphology all contribute to preservation potential for insects (Grimaldi and Engel 2005, Smith 2012, Smith et al. 2006). Although preservation of insects in the Kaiparowits Formation seems promising, the lack of insect body-fossil discoveries may be due to unsuitable aquatic chemistry, although further exploration is required. Nonetheless, trace fossils of insect herbivory are exceedingly abundant in the Kaiparowits Formation.

Insect trace fossils in the Kaiparowits Formation have been previously described in sedimentary rocks (Roberts and Tapanila 2006) and dinosaur bone (Roberts et al. 2007), but insect herbivory on fossil leaves is only now being documented (Maccracken et al. in review-a). Traces of insect herbivory on fossil leaves not only provide vital clues to what insect feeding guilds were present when insect body fossils are unknown (Labandeira et al. 2007c), but also are among of the richest sources for evidence of organisms interacting in the fossil record and often predate their respective body fossil record (Labandeira 2006a, Maccracken et al. in

review-b, Wilf et al. 2001). Fossil plant–insect traces are used to infer food web evolution and response to internal and external perturbations (Dunne et al. 2014, Wilf 2008); the presence and richness of insect feeding guilds (i.e. leaf miners, galling insects, piercing-and-sucking insects bearing stylet-like mouthparts) (Schachat et al. 2015, Schachat et al. 2014); diversity of damage types (Carvalho et al. 2014, Donovan et al. 2018, Donovan et al. 2014, Maccracken et al. in review-a); rarely to taxonomically identify damage patterns to a particular species or lineage of insect culprits (Maccracken et al. in review-b, Wilf et al. 2000); and host plant specialization (Donovan et al. 2016). However, few studies have measured plant–insect associations during the Late Cretaceous (ex. Arens and Gleason 2016), the majority of which document terminal Cretaceous fossil deposits (Donovan et al. 2016, Donovan et al. 2018, Donovan et al. 2014, Labandeira et al. 2007a, Labandeira et al. 2002a, Labandeira et al. 2002b, Wappler et al. 2009) or individual insect damage patterns (ex. Jud and Sohn 2016, Krassilov 2007, Krassilov 2008a, Labandeira 1998c, Vasilenko 2008, Wilf et al. 2000).

Here, we describe and quantify plant–insect from the JARS locality (DMNH I. 3725) in the Kaiparowits Formation, Utah, USA. The objectives of this study are to: 1) analyze the richness and intensity of insect damage on fossil leaves from the JARS locality of the Kaiparowits Formation; 2) identify any potential insect culprits responsible for the damage types; and 3) compare the richness and intensity of JARS insect damage to a previously documented Late Cretaceous taxon.

Geological Setting

The Campanian-aged Kaiparowits Formation (76.49 ± 0.14 to 74.69 ± 0.18 Ma) (Roberts et al. 2013) is located in southern Utah, USA (Figure 3.1). The formation now occurs within and outside the boundaries of the recently diminished Grand Staircase–Escalante National Monument (Eilperin 2017, Kolbert 2018, Light and Hale 2018, Miller 2018, Penn-Roco 2018, Underwood 2017). The Kaiparowits Formation comprises ~1005 m of alternating sandstones and mudstones, which preserve several depositional environments, such as channels, lakes, and a variety of

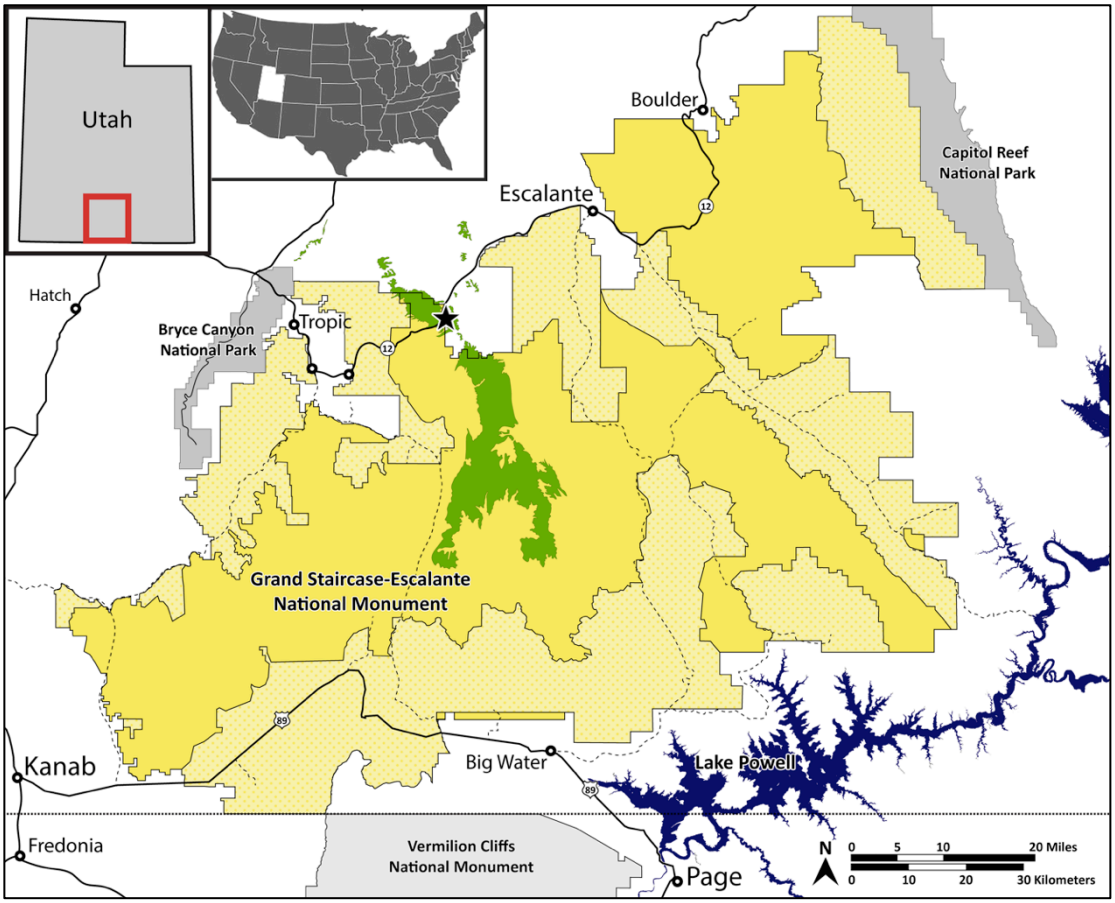


Figure 3.1: Map of the Kaiparowits Formation outcrop (green). Solid yellow denotes new boundaries for the Grand Staircase-Escalante National Monument (December 2017) and former monument areas are stippled in lighter yellow. DMNH loc.3725, the JARS locality, is denoted by a blue star. Map modified from Crystal et al. (2019).

floodplain deposits that include crevasse splays, perennial ponds, and oxbow lakes (Beveridge et al. 2020, Roberts 2007, Roberts et al. 2013).

The majority of paleobotanical localities occur in the middle member of the formation (ca. 90-110 to ca. 550 m) (Roberts 2007). The JARS locality, (DMNH I. 3725) occurs at 365 ± 20 m above the base of the formation (Figure 3.2). With an estimated depositional rate of 41 cm/1,000 years in calculating 40Ar/39Ar ages on sanidine crystals from volcanic ash beds (Roberts et al. 2013), we estimate the age of the JARS locality at 75.7 ± 0.05 Ma, which corresponds to the late Campanian Age (Walker et al. 2018). Specimens were collected in 2008 and are reposited at the Denver Museum of Nature & Science (DMNS) in Denver, Colorado, USA. The leaves occur as compression-impression fossils on mudstone, siltstone, and fine grained sandstone matrices (Locatelli et al. 2017, McMahon et al. 2016), and the JARS locality facies association is interpreted as forming in lacustrine settings (Roberts 2007).

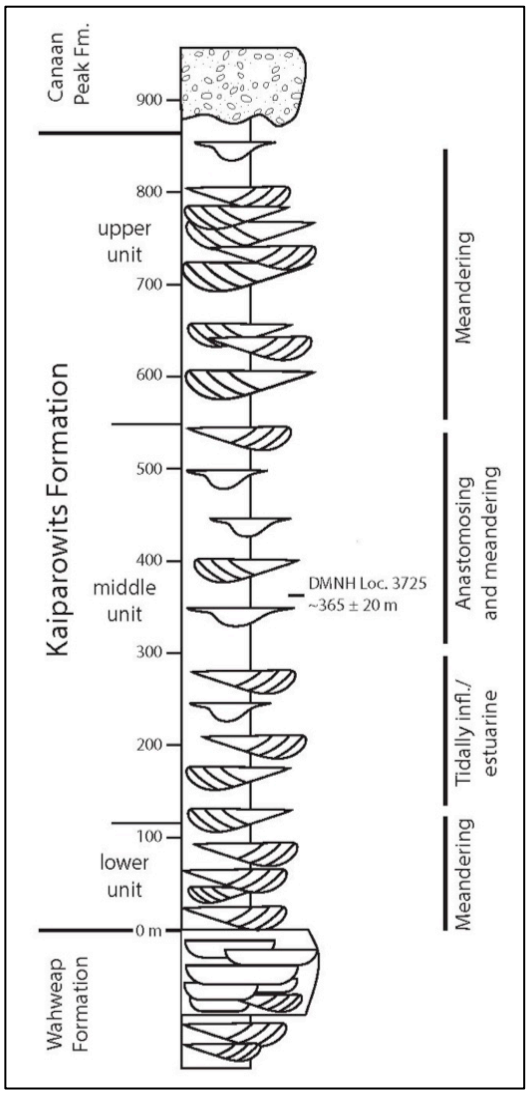


Figure 3.2: Stratigraphic column for the Kaiparowits Formation, Utah, USA, redrawn from Roberts (2007). The stratigraphic position of DMNH loc. 3725, where the JARS locality specimens were collected is noted.

Materials and Methods

All fossil plant specimens from the JARS locality that were at least 50% complete and identifiable were collected. Leaves were prepared to expose the entire leaf surface whenever possible, using Chicago pneumatic air scribes. Leaf specimens included in the analyses were morphotyped, a non-taxonomic categorization outlined in Johnson et al. (1989) and detailed in Chapter 2 of this dissertation. We did not distinguish between fossil leaves and leaflets, as they both represent distinct laminar structures. After being morphotyped, leaf specimens were analyzed for insect herbivory. We analyzed 719 fossil plant specimens, including seeds, reproductive structures and leaves from lycopsids, *Equisetum*, ferns, conifers, and monocotyledonous and dicotyledonous angiosperms.

Several criteria were used to separate insect herbivory and oviposition from physical damage, detritivory, and taphonomic processes: (1) reaction tissue produced by the plant in response to herbivory, often in the form of hypertrophy (cell size increase) and hyperplasia (cell multiplication) (Brues 1924, Johnson and Lyon 1991, MacKerron 1976, Vincent et al. 1990); (2) targeting of specific host plant taxa or particular plant organs, which are indicative of host plant specialization (ex. Gangwere 2017, Iannuzzi and Labandeira 2008, Kazakova 1985, Keen 1952); (3) recurring stereotypy of a damage pattern based on shape, size, and position of the damage on the plant (Bodnaryk 1992, Heron 2003); and (4) atypical and distinctive, micromorphological features associated with consumption of plant tissues (Labandeira et al. 2007c), for example vein strings linked to the inability of some mandibulate phytophagous insects to process tough vein tissue. After damage was

identified as herbivory, the damage was classified by functional feeding guild and specific pattern (damage type).

Qualitative insect herbivory was analyzed using the *Guide to Insect (and other) Damage Types on Compressed Plant Fossils* (Labandeira et al. 2007c). The guide is categorized into functional feeding groups, which are akin to insect feeding guilds. Within each functional feeding group are numbered damage types, each of which is a discrete, diagnosable damage pattern that is assigned a number. Damage types are designated by shape, size, extent, and location of herbivore damage and are scored for host specificity with respect to the plant host: 1 for specialized (monophagy) damage, 2 for intermediate (oligophagy) damage, and 3 for generalist (polyphagy) damage (Labandeira et al. 2007c). Convergent similarities in herbivore mouthparts and feeding behaviors rarely make genus or species level identification of the insect culprit possible, with the exception of some leaf mines, galls, margin feeding, and scale-insect feeding traces (ex. Maccracken et al. in review-b, Sarzetti et al. 2008, Wilf et al. 2000).

The two major groups of insect damage are endophytic feeding and ectophytic feeding. Endophytic feeding is divided into four functional feeding groups: piercing and sucking, galling, leaf mining, and oviposition. Endophytic feeding is the consumption of plants by insect herbivores from within a plant tissue, or by insects using their piercing-and-sucking mouthparts to penetrate into, and feed from within the plant organ. Ectophytic feeding is also divided into four functional feeding groups: hole feeding, margin feeding, skeletonization, and surface feeding. Ectophytic feeding is caused by insects with mandibulate mouthparts that chew plant

tissues. Additional functional feeding groups include seed predation, borings, pathogen infection, *Incertae sedis*, and domatia. Furthermore, while all functional feeding groups fall under the umbrella of plant—insect associations, not all are herbivory *per se*. Oviposition, *Incertae sedis*, and pathogen associations with plant hosts represent damage to plant organs that reduce photosynthetic potential and are not feeding, but nonetheless destroy photosynthetic tissue. Alternatively, plant–insect mutualisms, such as mite domatia, are not included in measurements of herbivory because mutualisms are not antagonistic to the host plant.

The quantitative measurements for insect herbivory in this study were richness of functional feeding groups and damage types, the percentage of insect damaged leaves, and the herbivory index, which is the proportion of surface area removed by an insect herbivore to the total surface area of the leaf. Leaf surface area was measured using Adobe Illustrator Draw© for iPad Pro and ImageJ (Rasband 2012). Piercing and sucking damage was particularly difficult to measure because puncture marks are often diminutive and can number from the tens to thousands. We measured the average puncture surface area for each leaf and multiplied that by the number of punctures on the leaf. Average puncture marks were below 0.025 mm^2. All metrics were measured for the total flora and for each plant taxon. The proportion of insect damaged leaves in a flora is known to be highly variable (Schachat et al. 2018), and although we present this metric, we do not use it for the purpose of comparisons.

All leaves were photographed using a Canon EOS 50D camera body with a Canon EF-D 60mm f/2.8 macro lens. Microphotographic images of insect damage were taken by an Olympus SZX12 microscope with an Olympus DP25 camera. Low

angle light produced by a Dolan-Jenner illuminator was used in some instances to enhance subtle insect damaged zones.

Damage-type richness by total surface area measured was documented with a sample-sized-based rarefaction. We used code developed by S. Schachat (Schachat et al. 2018) for *R* statistical software (R Development Core Team 2013), in which data were bootstrapped 5000 times at a confidence interval of 95%. To visualize the differences in suites of functional feeding groups between specimens, we used a nonmetric multidimensional scaling (NMDS) ordination, which employed a Bray-Curtis dissimilarity matrix. The results of the NMDS were shown an ordination plots of the nine plant hosts and functional feeding groups present at the JARS locality for the three most abundant plant hosts and nine most abundant plant hosts. Ellipses were drawn containing 84% of the points closest to the centroid of each of the nine plant host ellipses to represent 84% confidence intervals. The NMDS ordinations were produced by the "metaMDS" function of the vegan package, in *R* version 3.1.2 (R Development Core Team, 2013).

Results

Plant Diversity

The JARS locality (DMNH I. 3725) in the Kaiparowits Formation yielded a total of 719 identified fossil plant specimens, 589 of which were angiosperm specimens (Table 3.1) (Figure 3.3). These plant specimens constituted 70 morphotypes, which were categorized into: 1) seeds and reproductive material; 2)

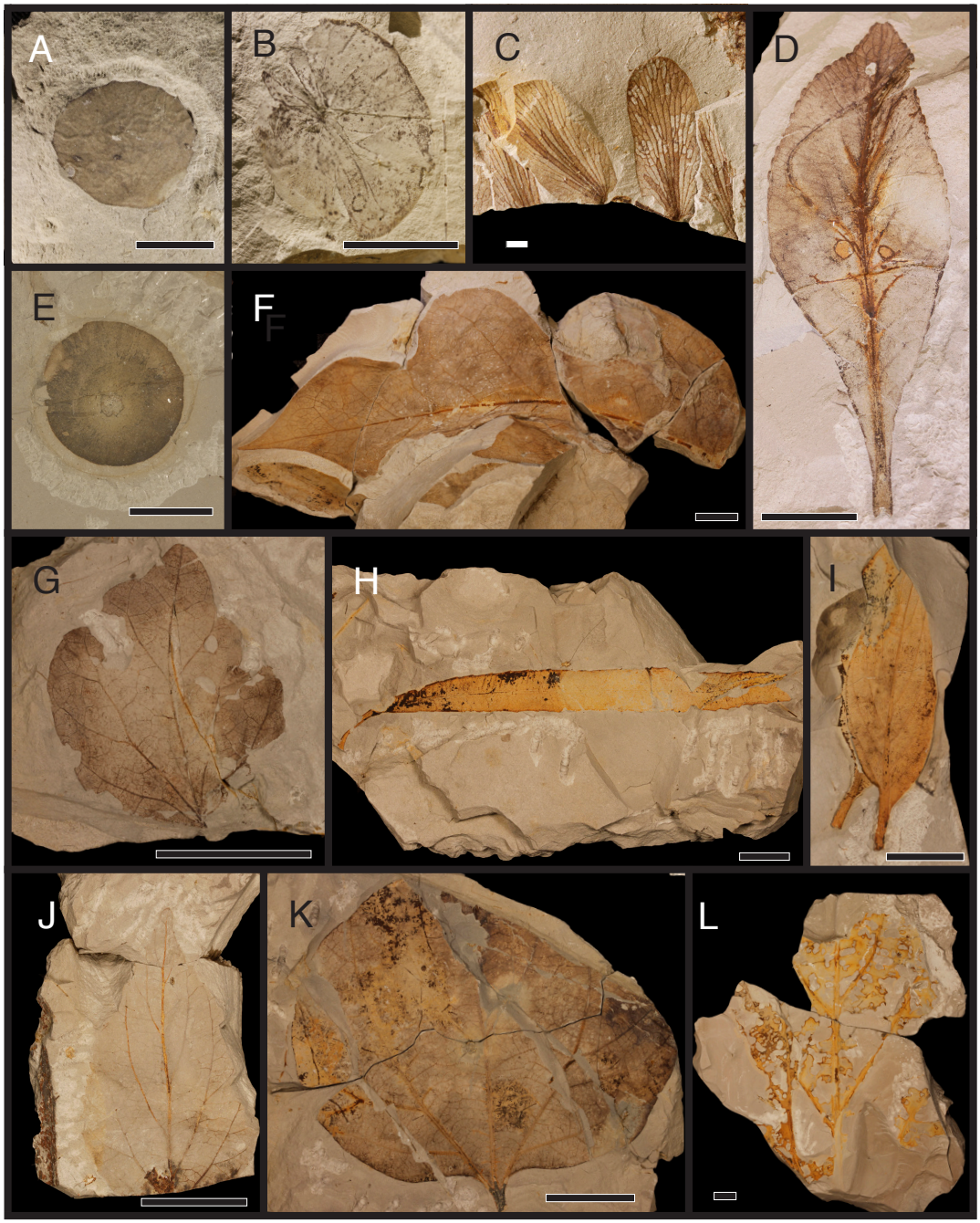


Figure 3.3: Taxonomically identifiable plant hosts and plant hosts with more than 20 specimens from the JARS locality. A, *Quereuxia* sp., plant host (PH)12.1 (DMNH EPI.45447); B, *Brasenites* sp., PH12.2 (DMNH EPI.45532); C, *Hydropteris* sp., PH7.4 (DMNH EPI.45533); D, PH16.1 (DMNH EPI.45468); E, *Cobbania* cf. *C. corrugata*, PH11.1 (DMNH EPI.45531); F, PH13.1 (DMNH EPI.45432); G, PH36.1 (DMNH EPI.45431); H, PH16.2 (DMNH EPI.45429); I, PH30.1 (DMNH EPI.45430); J, PH15.1 (DMNH EPI.45440); K, PH39.1 (DMNH EPI.45428); L, PH41.1 (DMNH EPI.45455). Black scale bar = 1 cm; white scale bar = 1 mm.

lycopods; 3) horsetails; 4) ferns; 5) conifers; 6) monocotyledonous angiosperms (monocots); and 7) dicotyledonous angiosperms (dicots). There were 49 dicot morphotypes, which we will refer to as plant hosts that included herbaceous, aquatic, vining, and woody life forms. There were four plant hosts that were also taxonomically identifiable: *Hydropteris* sp., an aquatic fern (Plant Host (PH) 7.4) (Figure 3.3 C); *Quereuxia* sp., a floating aquatic dicot (PH12.1) (Figure 3.3 A); *Cobbania* cf. *C. corrugata*, a floating aquatic monocot (PH11.1) (Figure 3.3 E); and *Brasenites* sp., a floating aquatic dicot (PH12.2) (Figure 3.3 B). All other plant hosts are, as yet, of unidentified and/or undescribed species.

Table 3.1: Summary of JARS locality morphotypes and specimens in each major taxonomic unit.

Major taxonomic category	**Number of morphotypes**	**Number of specimens**	**Percent of Morphotypes**	**Percent of Specimens**
Lycopoda	1	18	1.43	2.50
Equisetopsida	1	8	1.43	1.11
Pteridophytes	5	73	7.14	10.15
Coniferales	2	4	2.86	0.56
Angiospermophytina				
Reproductive organs	12	27	17.14	3.76
Monocot leaves	3	7	4.29	0.97
Dicot leaves	46	582	65.71	80.95
Total	70	719	-	-

Damage Intensity

In total, there were 654 insect damage occurrences across 318 total damaged specimens (44.23% of specimens herbivorized) at the JARS locality (Table 3.2). Because multiple damage types may occur on a single leaf specimen, there were more damage type occurrences than damaged specimens. Insect herbivory at JARS was

almost entirely on angiosperms, with scant or no damage on conifers, lycopods, horsetails, and plant reproductive organs. The damage that did occur on non-angiosperm specimens was restricted to generalist, ectophytic feeding, with the exception of seed predation and two galls. Insect damage on foliar angiosperm specimens of angiosperm foliage totaled 615 occurrences across 301 specimens (51.1% of angiosperms were herbivorized). Although all identifiable angiosperm specimens were analyzed for herbivory, for the results and discussion we focused on plant hosts with at least 20 specimens, a precedent set forth by previous herbivory studies (Currano 2009). These targeted plant hosts are: PH16.1, PH39.1, PH36.1, *Quereuxia* sp. (PH12.1), PH30.1, PH16.2, PH41.1, PH15.1, and PH13.1 (Figure 3.3 A, D, F–L).

The herbivory index, or the percent of surface area removed by the insect herbivore, was 3.97% for the JARS locality angiosperms (Table 3.3, Figure 3.4) and the 95% confidence interval was between 3.11% and 5.40%. Herbivory index calculations for individual plant hosts and the confidence interval ranges were highly variable for the 20 most abundant taxa; the plant host herbivory indices ranged between 0.68% and 10.54% (see Supplementary Figure 3.1 in Appendix C). Confidence intervals were very large for some taxa, especially those with limited total surface areas.

Diversity of Insect Damage

With a total of 12 functional feeding groups and the JARS locality, the only functional feeding group missing from JARS was wood borings, which is to be expected given that there are no wood specimens in the collection. The functional

Table 3.2: Richness of damage types, host specificities, and the number of damage occurrences per functional feeding group.

Functional Feeding Groups	**Generalist Damage Types**	**Intermediate Damage Types**	**Specialist Damage Types**	**Number of Occurrences**
Hole Feeding	DT1; DT2; DT3; DT4; DT5; DT7; DT78	DT8; DT50; DT51; DT57; DT63	DT126	294
Margin Feeding	DT12; DT13; DT143	DT15; DT26; DT198; DT214; DT271		124
Skeletonization	DT16; DT17	DT20; DT24	--	8
Surface Feeding	DT29; DT30; DT31	DT82	--	29
Piercing and Sucking	--	DT138	DT46; DT330	53
Galling		DT32; DT34; DT80; DT194	DT33; DT85	95
Leaf Mining			DT43; DT176; DT295	6
Oviposition	--	DT100; DT101	--	29
Seed Predation	--	DT74	--	3
Pathogen/Environment	DT114	DT58; DT221; DT281	DT229	6
Incertae sedis	DT106	--	--	2
Domatia			DT339	5
TOTAL: 12 FFGs; 51 Damage Types	17 Generalist Damage Types	24 Intermediate Damage Types	10 Specialist Damage Types	654 Occurrences

Table 3.3: Bulk floral data for the forty-nine angiosperm morphotypes from the Late Cretaceous (Campanian) JARS locality, Kaiparowits Formation.

Foliar morphotypes (abundance ranked)	Number of specimens	Specimens examined of total number (%)	Surface area examined of total number (%)	Total surface area (cm^2)	Herbivorized surface area (cm^2)	Proportion of total herbivor-ized specimens (%)	Herbivory index	Number of herbivor-ized specimens in flora	Proportion of herbivor-ized specimens (%)
16.1	95	16.13	9.33	49937.758	1110.037	13.68	2.22	42	44.21
39.1	64	10.87	17.72	94803.400	693.643	9.12	0.73	28	43.75
36.1	48	8.15	5.55	29701.524	1455.934	9.77	4.90	30	62.50
12.1	41	6.96	1.04	5543.442	211.591	6.84	3.82	21	51.22
16.2	36	6.11	2.55	13624.559	92.764	3.26	0.68	10	27.78
30.1	36	6.11	7.04	37656.977	888.042	3.58	2.36	11	30.56
15.1	34	5.77	3.69	19751.933	632.351	4.56	3.20	14	41.18
41.1	34	5.77	20.18	107993.603	11378.745	10.10	10.54	31	91.18
13.1	30	5.09	6.58	35198.769	704.196	6.51	2.00	20	66.67
24.2	17	2.89	4.57	24444.698	424.267	3.91	1.74	12	70.59
25.1	16	2.72	2.09	11193.095	984.339	4.23	8.79	13	81.25
29.2	16	2.72	2.18	11651.556	73.114	2.28	0.63	7	43.75
41.4	12	2.04	2.12	11352.245	381.841	2.93	3.36	9	75.00
16.4	10	1.70	0.46	2475.621	8.498	1.63	0.34	5	50.00
24.1	10	1.70	1.89	10097.553	378.054	2.61	3.74	8	80.00
24.3	10	1.70	1.95	10414.686	23.922	1.63	0.23	5	50.00
32.2	7	1.19	0.67	3583.516	11.767	1.30	0.33	4	57.14
16.5	5	0.85	0.36	1917.809	9.564	1.30	0.50	4	80.00
29.1	5	0.85	0.49	2598.665	15.473	0.65	0.60	2	40.00

31.1	5	0.85	0.77	4126.236	161.647	0.98	3.92	3	60.00
31.2	5	0.85	0.19	1017.009	132.248	0.65	13.00	2	40.00
22.1	4	0.68	0.56	2997.324	123.303	0.98	4.11	3	75.00
24.4	4	0.68	0.73	3912.207	3.152	0.65	0.08	2	50.00
33.1	4	0.68	0.32	1706.432	167.958	1.30	9.84	4	100
11.1	3	0.51	0.23	1229.096	0.837	0.33	0.07	1	33.33
11.2	3	0.51	0.36	1943.496	20.121	0.33	1.04	1	33.33
22.2	3	0.51	0.39	2094.474	38.196	0.65	1.82	2	66.67
23.1	3	0.51	1.07	5742.184	215.431	0.33	3.75	1	33.33
30.2	3	0.51	0.25	1353.848	0.28	0.33	0.02	1	33.33
14.1	2	0.34	0.71	3773.891	158.433	0.33	4.20	1	50.00
23.2	2	0.34	0.62	3340.798	19.623	0.33	0.59	1	50.00
27.3	2	0.34	0.25	1328.499	190.145	0.33	14.31	1	50.00
28.3	2	0.34	0.03	181.625	0	0	0	0	0
35.1	2	0.34	0.22	1198.434	0	0	0	0	0
35.2	2	0.34	0.37	1954.827	0	0	0	0	0
11.3	1	0.17	0.14	740.14	0	0	0	0	0
12.2	1	0.17	0.06	344.107	9.544	0.33	2.77	1	100
17.1	1	0.17	0.63	3359.873	21.175	0.33	0.63	1	100
18.1	1	0.17	0.04	187.942	0.417	0.33	0.22	1	100
19.1	1	0.17	0.02	123.959	1.941	0.33	1.57	1	100
24.5	1	0.17	0.13	700.836	81.854	0.33	11.68	1	100
29.3	1	0.17	0.15	805.603	0	0	0	0	0
30.3	1	0.17	0.07	364.178	0	0	0	0	0
31.3	1	0.17	0.12	650.654	0	0	0	0	0
32.1	1	0.17	0.45	2388.515	173.784	0.33	7.28	1	100
34.1	1	0.17	0.25	1351.912	105.628	0.33	7.81	1	100

37.4	1	0.17	0.25	1356.058	99.854	0.33	7.36	1	100
41.2	1	0.17	0.12	664.354	0	0	0	0	0
41.3	1	0.17	0.05	247.203	0	0	0	0	0
Totals/percent sums & averages	**589**	**100.03**	**100.01**	**535127.123**	**21230.349**	**100.05**	**3.96**	**307**	-

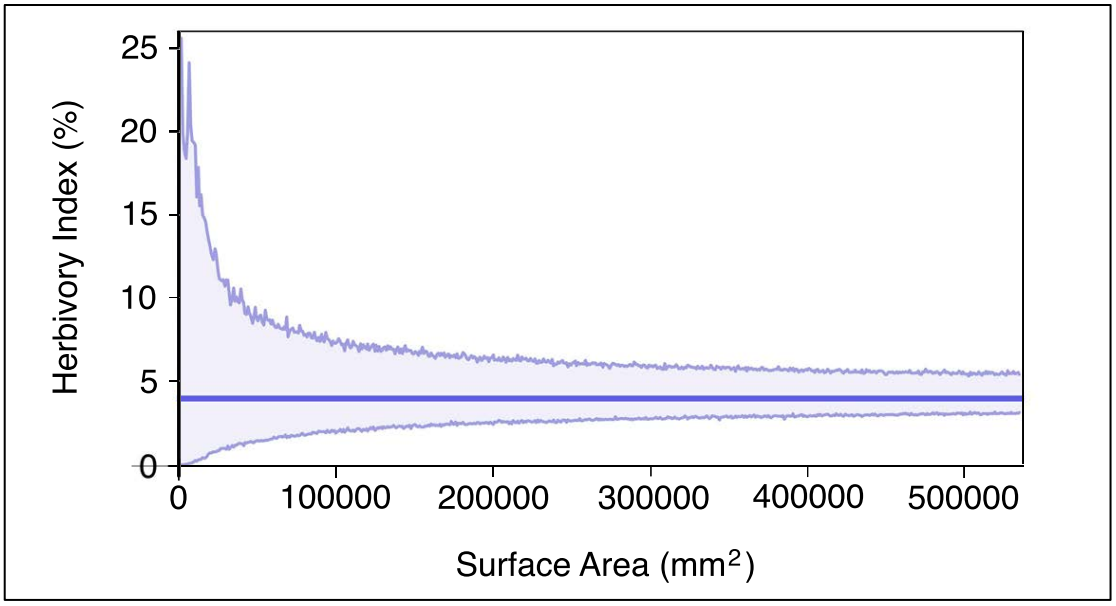


Figure 3.4: Herbivory index for the JARS locality. Center line represents the herbivory index and the upper/lower boundaries represent the 95% confidence interval range.

feeding groups were: hole feeding, margin feeding, skeletonization, surface feeding, piercing and sucking, galling, oviposition, leaf mining, seed predation, pathogen, *Incertae sedis*, and domatia (Table 3.2). The number of damage types per functional feeding group ranged from one to 13, with a total of 51 damage types (Table 3.2). Among the angiosperm specimens there were a total of 49 damage types, the majority of which were ectophytic feeding damage types (455 occurrences, 69.6% of all occurrences) (Figure 3.5).

The 29 ectophytic damage types at JARS are categorized into four functional feeding groups: hole feeding, margin feeding, skeletonization, and surface feeding. Hole feeding is the perforation through the leaf, including both adaxial and abaxial surfaces, that does not connect with the margin of the leaf. Hole feeding in the JARS locality was common and diverse, with thirteen damage types and 294 instances (Table 3.2; Figure 3.6). The most common hole-feeding damage types were circular

to ellipsoidal holes with diameters from <1 mm to >5 mm (DT1, DT2, DT4) (Figure 3.6 A) and polylobate holes from 1 mm to > 5 mm (DT3, DT5) (Figure 3.6 A, D, E). Slot feeding damage types included parallel-sided, curvilinear to rectilinear perforations (DT7) (Figure 3.6 A), rectilinear slots with parallel sides (DT8) (Figure 3.6 C), and overlapping slots forming a large, angulate hole (DT51) (Figure 3.6 J). Patterns of hole feeding included linear series of holes adjacent to a primary vein (DT50) (Figure 3.6 G), holes at the convergence of the primary veins (DT57) (Figure 3.6 H), and ellipsoidal holes connected by swaths of dark, necrotic tissue (DT126)

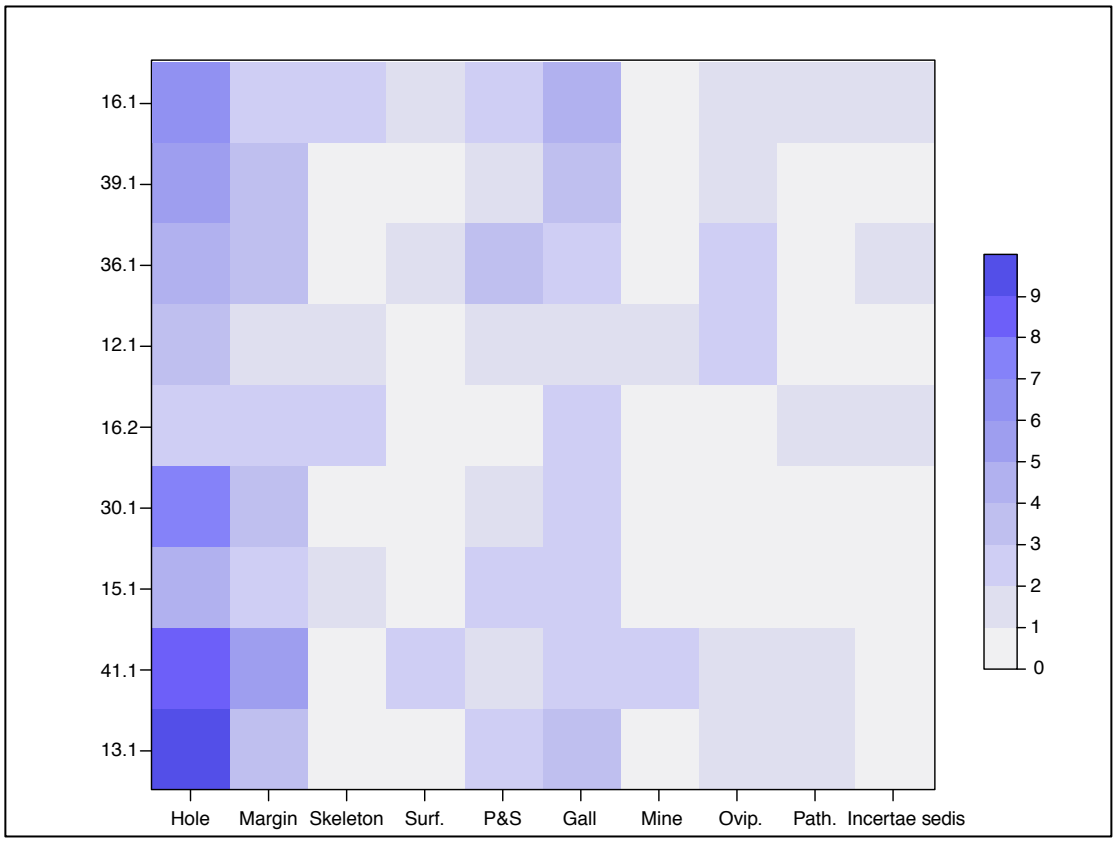


Figure 3.5: Heat map plot for the richness of damage types found on each plant host (Y-axis) by functional feeding group (X-axis). The number of damage types range from zero (lightest purple) to nine damage types (darkest purple).

(Figure 3.6 B). Finally, hole feeding included a primary vein suspended by hole feeding on either side (DT63) (Figure 3.6 F) and large areas of foliar tissue removed between secondary veins (DT78) (Figure 3.6 I).

Margin feeding is the consumption of the entire thickness of the lamina, which occurs along the margin of the leaf lamina. There were eight distinct margin feeding damage types at the JARS locality (Table 3.2; Figure 3.7). The most common margin feeding damage types were circular excisions (DT12) (Figure 3.7 H), excision of the leaf apex (DT13) (Figure 3.7 G), a deep excision of the margin that expanded as it approached the midline (DT15) (Figure 3.7 E), and a deep excision that narrowed towards the midline (DT198) (Figure 3.7 F). Other margin feeding damage types included the removal of large swaths of leaf margin that left veins intact (DT26) (Figure 3.7 C), a series of cuspate excisions with unherbivorized leaf margin separating each cuspule (DT143) (Figure 3.7 A), serial and adjoining cuspate excisions (DT214) (Figure 3.7 D), and the removal of over 50% of the laminar surface area with distinct cuspate feeding around the entire leaf (DT271) (Figure 3.7 B).

Skeletonization, similar to hole feeding, entails the consumption of the entire thickness of the leaf, but veins of various orders are left intact by the herbivore (Figure 3.8 A–C, E). There were four skeletonization damage types, the most common of which was the removal of interveinal tissue without a reaction rim present (DT16) (Figure 3.8 B). Also found at the JARS locality was the removal of interveinal tissue surrounded by a pronounced reaction rim (DT17) (Figure 3.8 C),

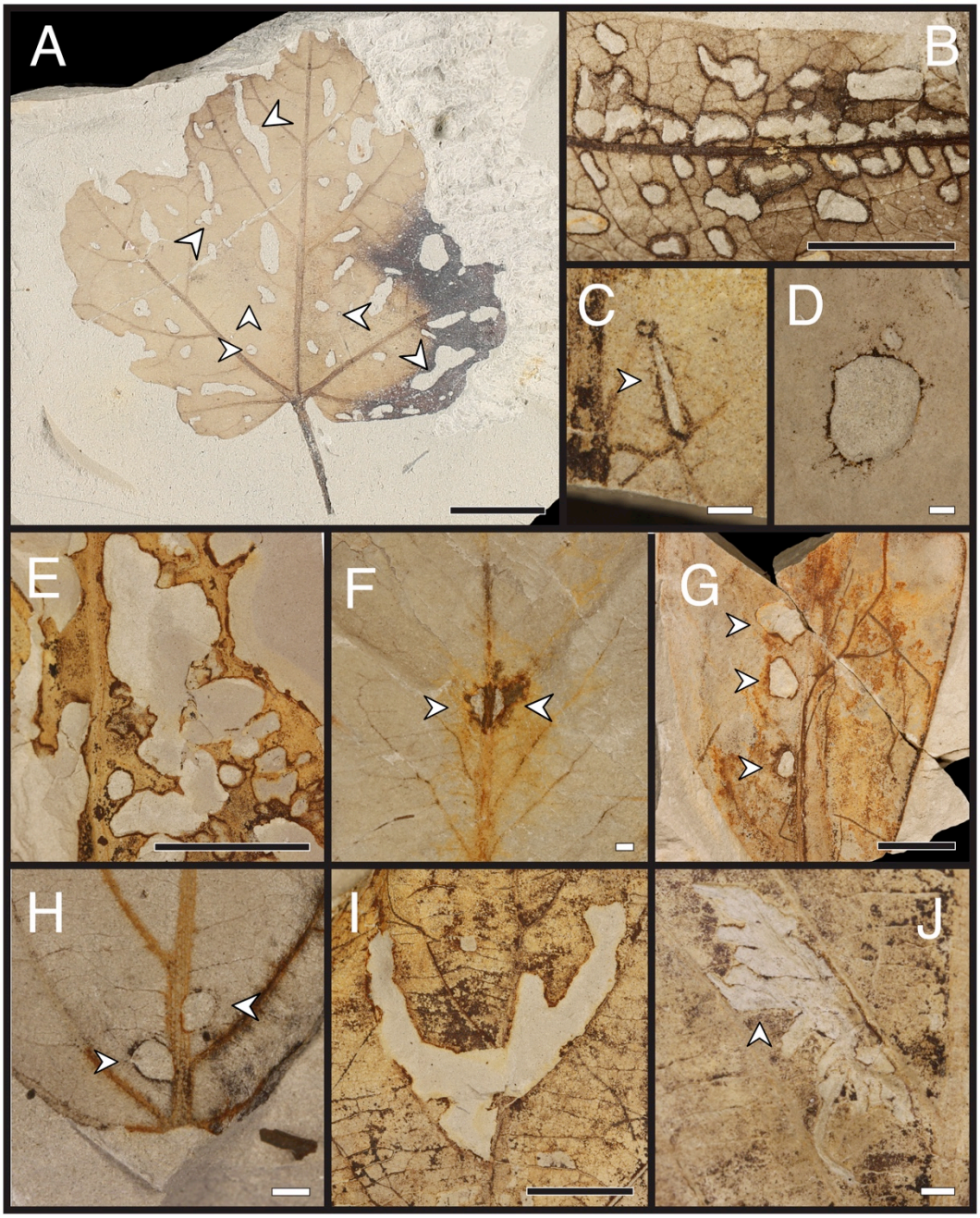


Figure 3.6: Hole feeding damage types found at the JARS locality, Kaiparowits Formation (Utah, USA). A, Arrows denote hole feeding damage starting from top center and proceeding clockwise: elongate hole that lacks parallel sides (DT7, plant host (PH) 16.1, DMNH EPI.45452), a circular hole < 1 mm in diameter (DT1, PH33.1, DMNH EPI.45530), circular hole between 1 and 2 mm in diameter (DT2, PH33.1, DMNH EPI.45530), polylobate hole between 1 and 5 mm in diameter (DT3, PH33.1, DMNH EPI.45530). B, Circular to polylobate holes surrounded and connected by necrotic tissue (DT126, PH25.1, DMNH EPI.45537). C, A long, parallel-sided hole (DT8, PH33.1, DMNH EPI.45530). D, A circular hole > 5 mm in diameter (DT4, PH41.1, DMNH EPI.45455). E, Polylobate holes > 5 mm in diameter

(DT5, PH41.1, DMNH EPI.45456). F, Hole feeding on either side of a primary vein (DT63, PH16.1, DMNH EPI.45459). G, A series of three holes along a primary vein (DT50, PH13.1, DMNH EPI.45457). H, Holes at the convergence of major veins (DT57, PH15.1, DMNH EPI.45471). I, Hole feeding on entire intercostal areas (DT78, PH30.1, DMNH EPI.45466). J, Slot feeding holes joined together to form a large, angulate hole (DT51, PH30.1, DMNH EPI.45441). Black scale bar = 1 cm; white scale bar = 1 mm.

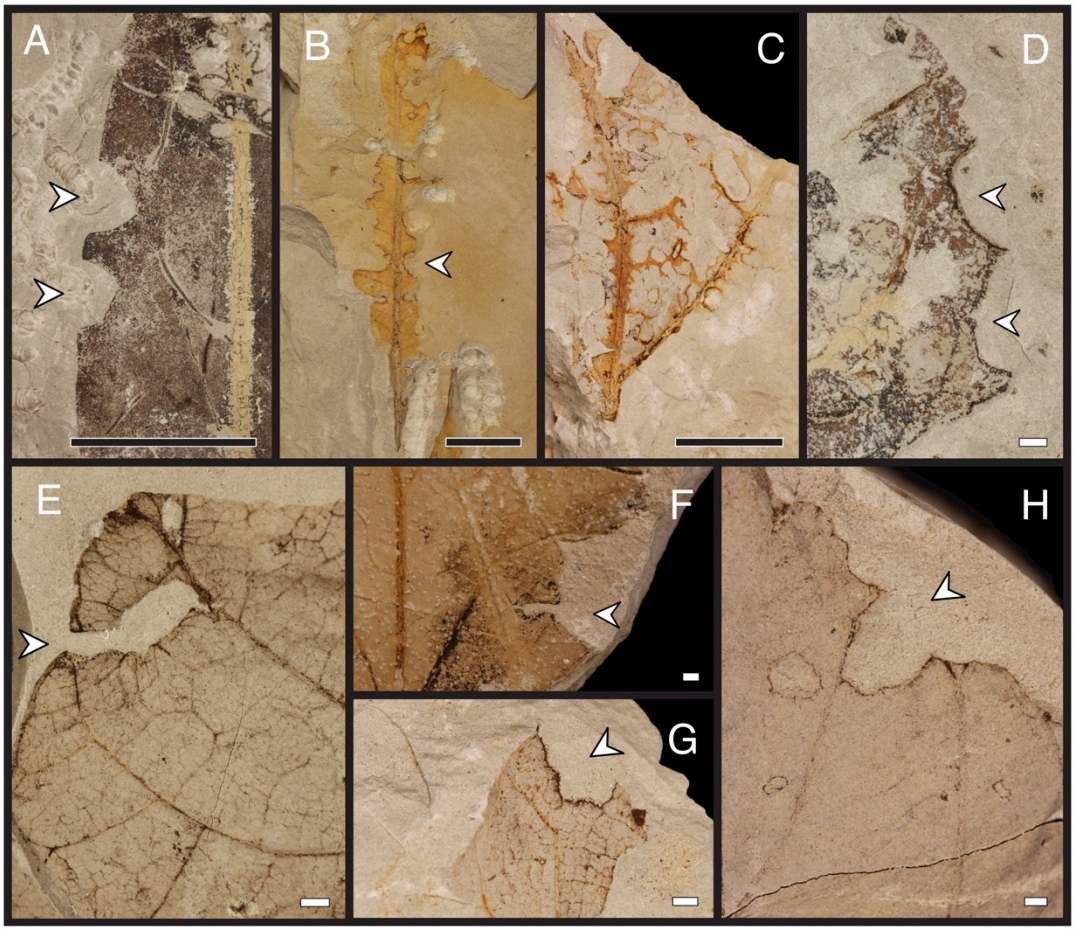


Figure 3.7: Margin feeding damage types found at the JARS locality. A, Small cuspate incisions along the margin with a portion of the leaf margin preserved between the cusps (DT143, plant host (PH) 24.5, DMNH EPI.45443). B, Removal of the margin with cuspate edges where at least 50% of the leaf lamina is consumed (DT271, PH25.1, DMNH EPI.45449). C, Extreme removal of the leaf margin wherein large portions of the lamina are consumed, except for major veins (DT26, PH41.1, DMNH EPI.45437). D, Broad cuspate incisions connected to one another (DT214, PH25.1, DMNH EPI.45469). E, Removal of the leaf margin that expands towards the midvein (DT15, PH39.1, DMNH EPI.45426). F, Incision of the leaf margin that narrows towards the midvein (DT198, PH29.2, DMNH EPI.45536). G, Removal of leaf apex (DT13, PH36.1, DMNH EPI.45467). H, Removal of the leaf margin within a 180º arc (DT12, PH34.1, DMNH EPI.45451). Black scale bar = 1 cm; white scale bar = 1 mm.

elongate strings of skeletonized tissue (DT20) (Figure 3.8 A), and oval patches of skeletonized tissue (DT24) (Figure 3.8 E).

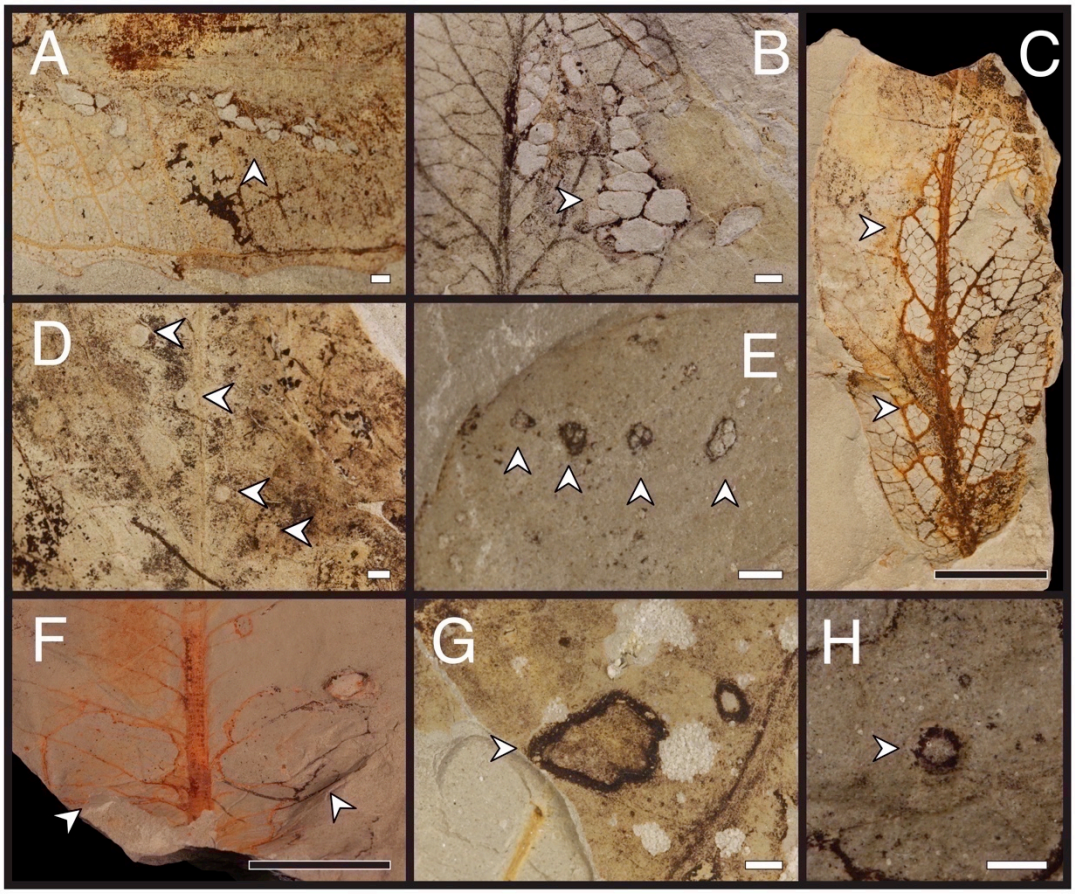


Figure 3.8: Skeletonization and surface feeding damage types found at the JARS locality. A, Linear removal of leaf lamina with veins intact (DT20, plant host (PH) 16.2, DMNH EPI.45435). B, Herbivory of leaf lamina without consumption of the vein network (DT16, PH16.1, DMNH EPI.45442). C, Herbivory of the leaf lamina with maintenance of the vein network, and a pronounced reaction rim surrounding the herbivorized areas (DT17, PH16.1, DMNH EPI.45458). D, Removal of the leaf surface without a reaction rim produced by the plant (DT29, PH24.2, DMNH EPI.45463). E, Circular patches of skeletonization in a linear projection (DT24, PH12.1, DMNH EPI.45454). F, Surface feeding patches that are symmetrically arranged around the primary vein (DT82, PH24.1, DMNH EPI.45535). G, Removal of the leaf surface with a polylobate reaction rim (DT30, PH41.1, DMNH EPI.45427). H, Removal of the leaf surface accompanied by a circular reaction rim (DT31, PH41.1, DMNH EPI.45453). Black scale bar = 1 cm; white scale bar = 1 mm.

The final ectophytic feeding group was surface feeding, or the consumption of either the abaxial or adaxial surface of the leaf lamina (Figure 3.8 D, F–H). There were four described examples of surface feeding, the most common of which was the removal of surface tissue with no or minimal reaction rim present (DT29) (Figure 3.8 D). The three other surface feeding damage types were: the removal of surface tissue with a polylobate reaction rim (DT30) (Figure 3.8 G), the removal of surface tissue with a circular reaction rim (DT31) (Figure 3.8 H), and polylobate surface feeding that was symmetrical about the primary vein (DT82) (Figure 3.8 F).

Endophytic feeding damage, made by insect herbivores that feed upon internal plant tissues, were present at modest levels in the JARS locality. There were a total of fourteen damage types and 183 instances belonging to the four function feeding groups of piercing and sucking, leaf mining, galling, and oviposition (Table 3.2). In general, the proportion of intermediate and specialist damage is greater in the endophytic functional feeding groups than the ectophytic feeding groups (Table 3.2).

Piercing-and-sucking insects puncture and siphon cells and fluid using elongate, stylet mouthparts. There were three piercing-and-sucking damage types found at the JARS locality (Figure 3.9 G–H). Generic stylet punctures resulting in small (< 2 mm) circular craters (DT46) were most common (Figure 3.9 G), followed by a series of three or more punctures (DT138) (Figure 3.9 F), and high densities of small (usually < 1 mm), carbonized punctures on tertiary venation (DT330) (Figure 3.9 H). DT330 is distinct from pathogen damage and leaf oil glands because the punctures are targeted preferentially along tertiary veins, unlike fungal spots, and often are not evenly spaced or patterned as are oil glands.

Oviposition, or egg laying into foliar tissue, was most common on the floating aquatic dicot *Quereuxia* sp. (PH12.2) (15 of the 29 oviposition occurrences at JARS). There were two oviposition damage types: oval oviposition scars arranged in parallel rows (DT100) (Figure 3.9 E), and oval oviposition scars that are not in a particular arrangement (DT101) (Figure 3.9C).

Mines are produced by insect larvae that live and consume the plant organ from within, either in serpentine patterns, blotch patterns, or a combination of the two. There were three types of leaf mines found at the JARS locality and a total of six leaf-mining occurrences. The first mine was serpentine, packed with solid frass, a modest width expansion, and about 1 mm in length (DT43) (Figure 3.9 A). A second mine consisted of a short trajectory (< 1 cm in length) with no visible frass that began with a serpentine phase and ended in a relatively large blotch phase (DT176) (Figure 3.9 D). The third leaf mine was a blotch mine that had a polylobate margin and no visible frass (DT295) (Figure 3.9 B).

Galls are envelopes of plant tissue elicited by a number of organisms, including insects and mites. Insect-mediated galls often provide nutrient supply and protection for the gall inhabitant. There were six gall damage types found at the JARS locality (Figure 3.10). The most frequently encountered galls were spheroidal to ellipsoidal in shape and occurred on the leaf lamina, which either avoided major veins (DT32) (Figure 3.10 E), occurred on primary veins (DT34) (Figure 3.10 D), or on secondary veins (DT33) (Figure 3.10 C). Other gall damage types included hemispheroidal galls (< 1 mm in diameter) that were tightly clustered (DT80) (Figure

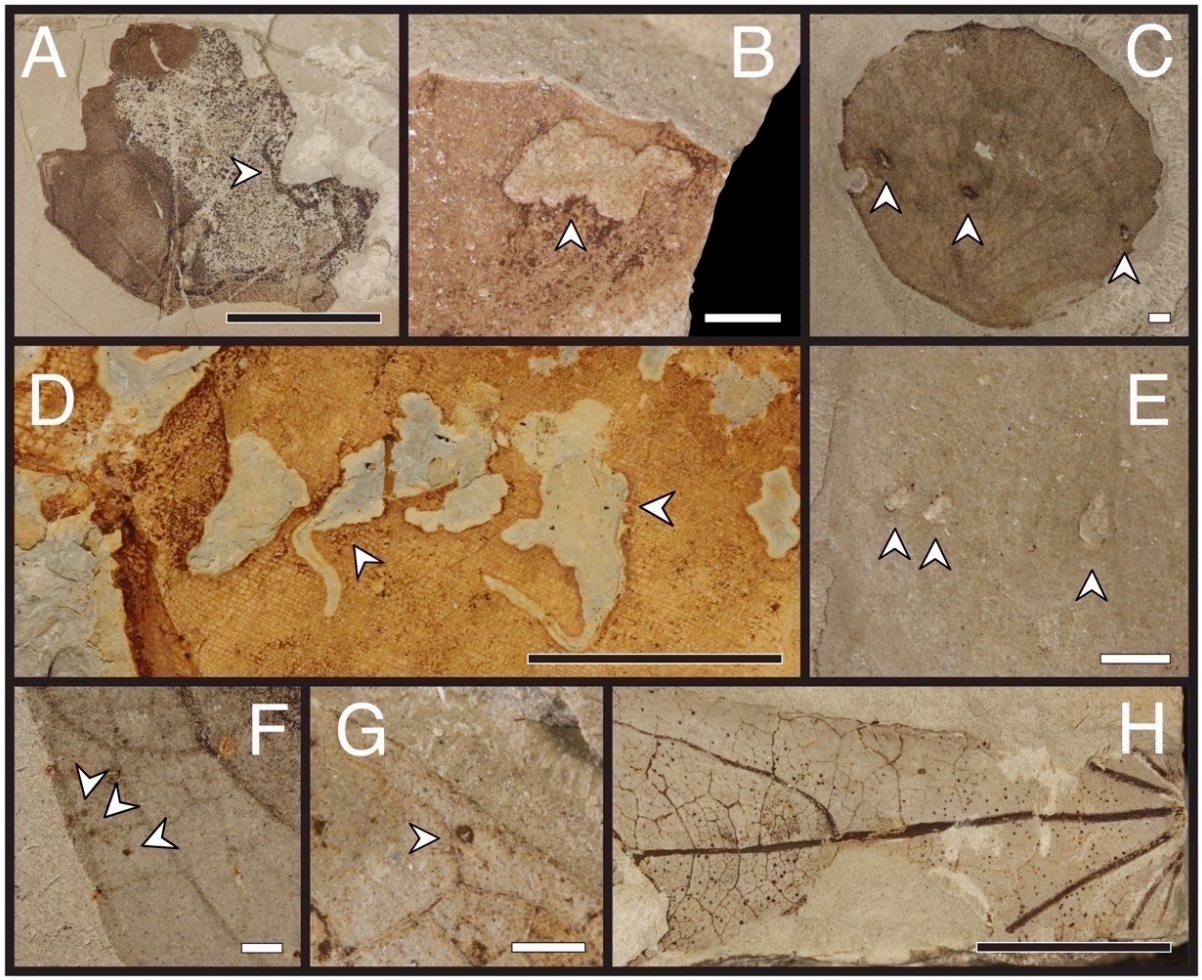


Figure 3.9: Leaf mining, oviposition, and piercing and sucking damage types found at the JARS locality. A, Two serpentine mines with solid frass throughout and modest width expansion (DT43, plant host (PH) 31.2, DMNH EPI.45464). B, A blotch mine with polylobate margin and frass absent (DT295, PH12.1, DMNH EPI.45434). C, Oviposition scars occurring on the leaf lamina in no discernable pattern (DT101, PH12.1, DMNH EPI.45447). D, Two, short mines with an initial serpentine phase and a relatively large terminal chamber (DT176, PH41.1, DMNH EPI.45460). E, Oviposition scars arranged parallel to one another (DT100, PH12.1, DMNH EPI.45454). F, Three punctures along the margin of the leaf (DT138, PH16.1, DMNH EPI.45448). G, A puncture < 1 mm in diameter (DT46, PH36.1, DMNH EPI.45438). H, Numerous, small punctures oriented on tertiary venation (DT330, PH36.1, DMNH EPI.45470). Black scale bar = 1 cm; white scale bar = 1 mm.

3.10 A), ellipsoidal galls that occurred on the midvein (DT85) (Figure 3.10 F), and crater-like attachment points of deciduous galls (DT194) (Figure 3.10 B).

Several functional feeding groups were outside the realm of endophytic and ectophytic feeding groups. These functional feeding groups included seed predation, pathogen infection, *Incertae sedis*, and domatia, which in total encompassed eight damage types (Figure 3.11). There was a single seed predation damage type, which consisted of small (< 0.5 mm in diameter) pits in the seed surface (DT74) (Figure

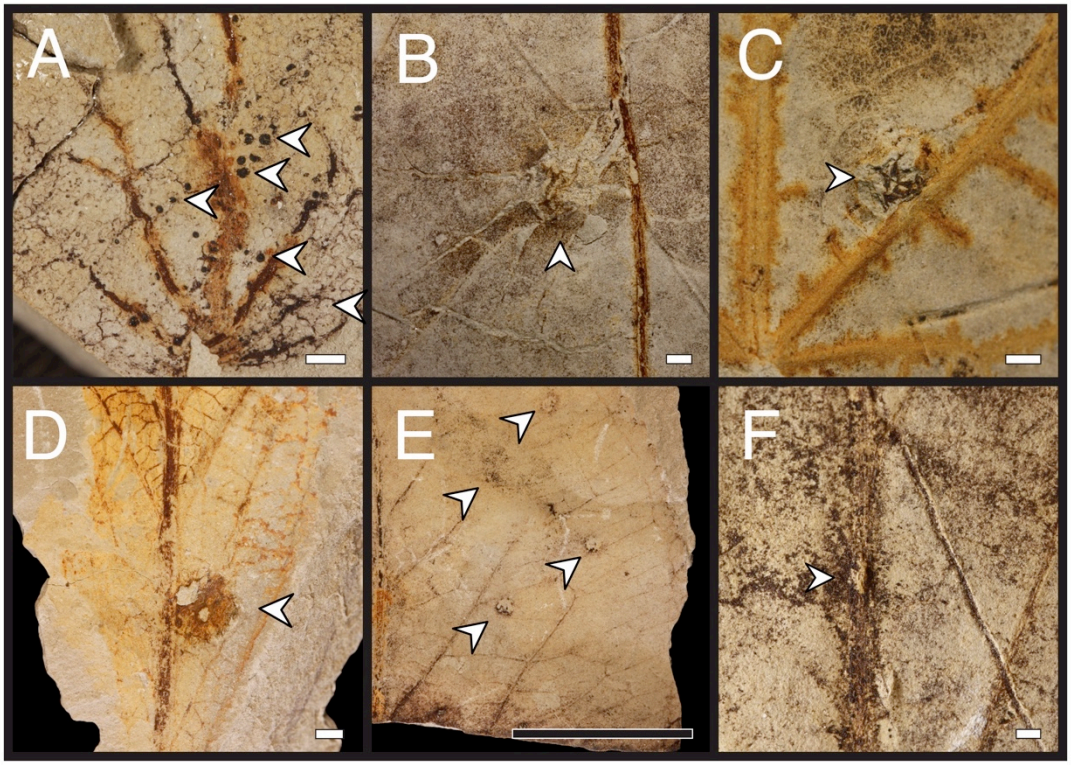


Figure 3.10: Insect gall damage types found at the JARS locality. A, Small, hemispheroid galls of high density on the leaf surface (DT80, plant host (PH) 32.2, DMNH EPI.45433). B, A crater left behind by a deciduous gall (DT194, PH24.2, DMNH EPI.45461). C, A circular gall located on secondary veins (DT34, PH32.2, DMNH EPI.45450). D, A circular gall located on primary veins (DT33, PH16.1, DMNH EPI.45444). E, Circular galls on the leaf lamina that avoid primary and secondary veins (DT32, PH16.1, DMNH EPI.45445). F, An ellipsoidal gall located on a primary vein (DT85, PH29.2, DMNH EPI.45436). Black scale bar = 1 cm; white scale bar = 1 mm.

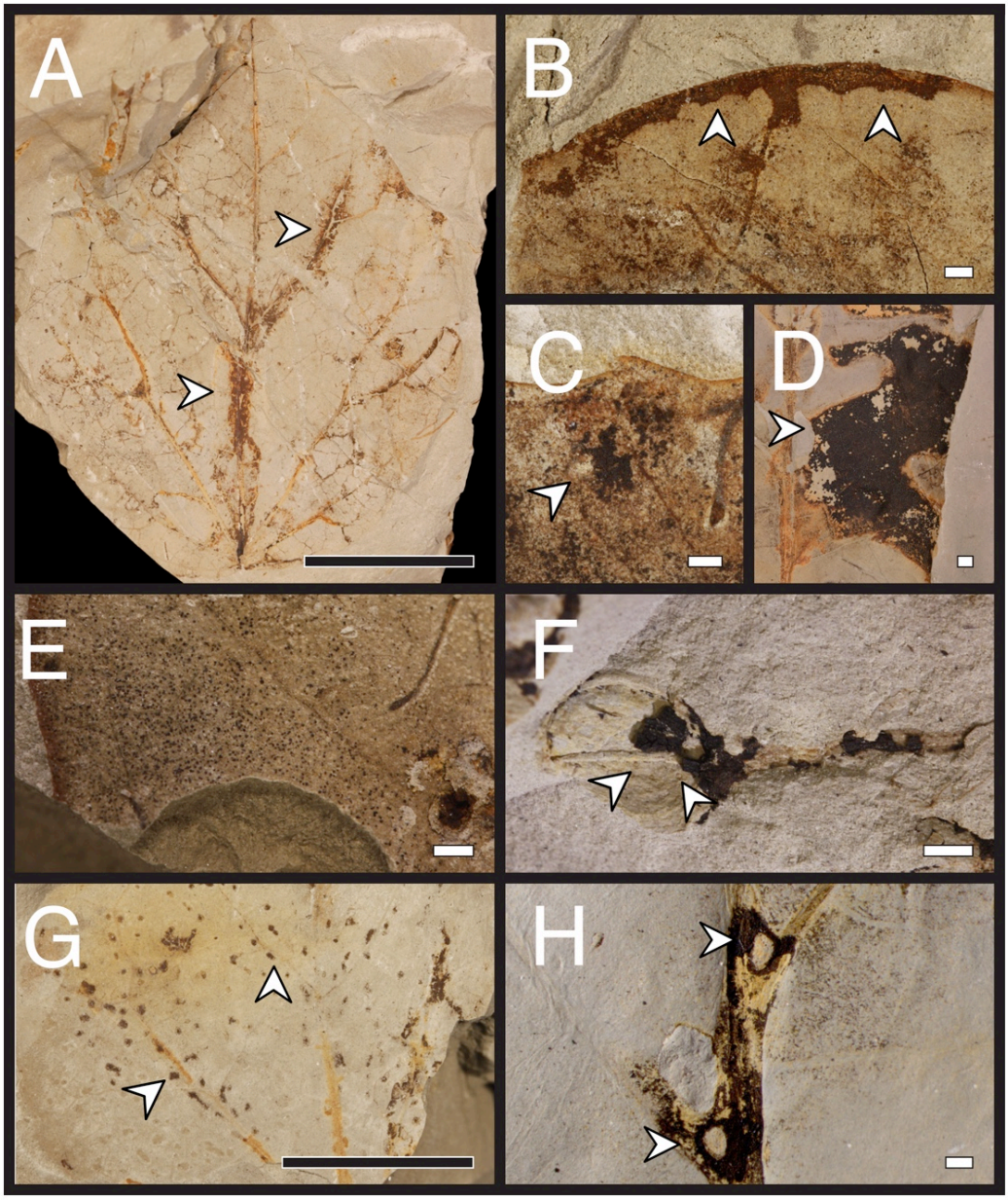


Figure 3.11 (following page): Pathogen damage, seed predation, *Incertae sedis*, and mite domatia found at the JARS locality in the Kaiparowits Formation (Utah, USA). A, Fungal damage along primary and secondary veins (DT221, plant host (PH) 36.1, DMNH EPI.45462).B, Fungal damage along the leaf margin (DT114, PH13.1, DMNH EPI.45472). C, *Incertae sedis* damage consisting of a pockmarked, roughened area (DT106, PH16.2, DMNH EPI.45447). D, Polylobate necrotic areas likely caused by a fungus (DT58, PH41.1, DMNH EPI.45427). E, Small, circular to ovoidal fungal spots in high density (DT281, PH13.1, DMNH EPI.45465). F, Seed predation with several small, circular pits (DT74, PH3.2, DMNH EPI.45534). G, Circular to polylobate fungal spots in medium density (DT229, PH36.1, DMNH EPI.45439). H, Mite domatia at the vein axils (DT339, PH41.1, DMNH.45456). Black scale bar = 1 cm; white scale bar = 1 mm.

3.11 F). Pathogen infection, usually associated with fungal infection, at JARS was relatively diverse yet uncommon, represented by five damage types and six occurrences. Fungal infection with polylobate margins (DT58) (Figure 3.11 D), necrotic tissue along the margin the leaf (DT114) (Figure 3.11 B), necrotic tissue along the primary and secondary veins (DT221) (Figure 3.11 A), small (< 1 mm), polylobate necrotic spots in clusters (DT229) (Figure 3.11 G), and very small spots of fungal necroses (< 0.5 mm) along major leaf veins and or margins (DT281) (Figure 3.11 E). Finally, one damage type of *Incertae sedis* (DT106) (Figure 3.11 C), which will likely be reassigned in the future and one type of mite domatia (DT339) (Figure 3.11 H) were discovered.

Rarefaction for the richness of damage types by total surface area was calculated for the nine most common plant hosts at the JARS locality (Figure 3.12). Among individual plant hosts, the confidence intervals of most specimens overlapped and were not significantly different, with one notable exception. PH39.1 had a lower richness of damage types compared to PH41.1, PH12.1, and PH16.1. Additional sampling surface areas for many of the plant hosts will likely be needed to differentiate damage-type richnesses between the taxa. It is worth noting here that herbivory index, which is often not present in plant–insect associational studies due to the time-consuming nature of surface area measurements, standardizes leaf size, as shown here with the differences between the large-leaved PH41.1 and small-leaved PH12.1. Rarefaction by specimen count would yield tenuous curves considering the difference in average leaf size between several of the plant hosts.

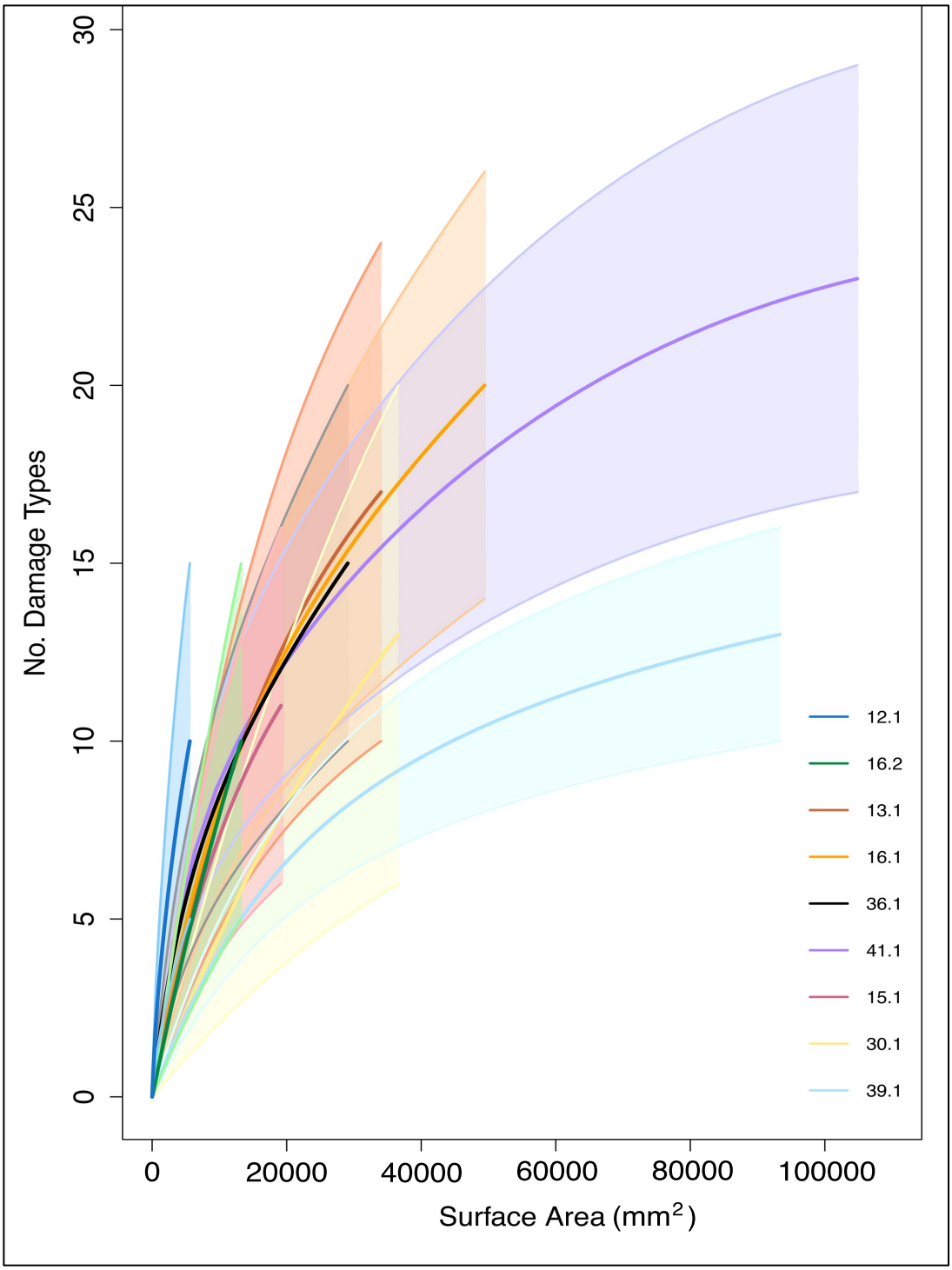


Figure 3.12: Rarefaction analysis of damage-type richness (Y axis) by surface area (X axis) for the nine individual plant hosts with > 20 specimens.

NMDS ordinations plots illustrated the predominant associations between the nine common plant hosts and the general categories of herbivorous insect damage (Figures 3.13–3.14). The plant host most associated with oviposition was *Quereuxia* sp. (PH12.1), whereas PH36.1 was most closely associated with piercing and sucking,

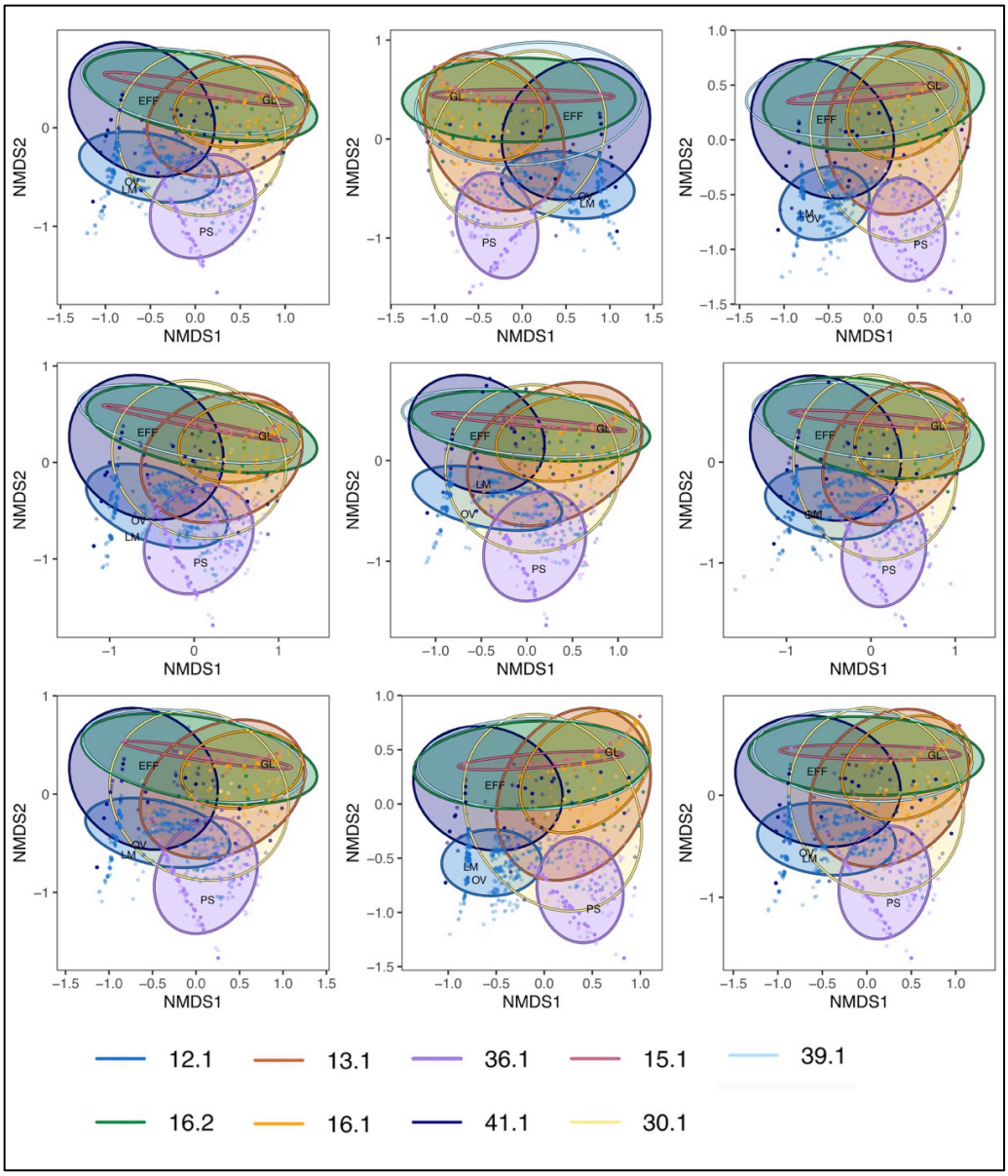


Figure 3.13: Non-metric multidimensional scaling (NMDS) ordination with elipses, which include 84% of the datapoints closest to the centroid, for the nine dominant plant hosts (with at least a total of 5,000 mm^2) and functional feeding groups present at the JARS locality. EFF is external foliage feeding, LM is leaf mining, GL is galling, IS is *Incertae sedis*, and OV is oviposition.

and PH16.2 trended towards pathogen and *Incertae sedis* damage (Figure 3.13). The elipses, which captured 84% of data points closest to the centroid, showed that PH36.1, PH12.1, and PH41.1 also occupied relatively distinct regions of the morphospace (Figure 3.14). The rest of the plant hosts (PH30.1, PH15.1, K16.1, PH39.1, and PH13.1) were clustered together with galling and external foliage

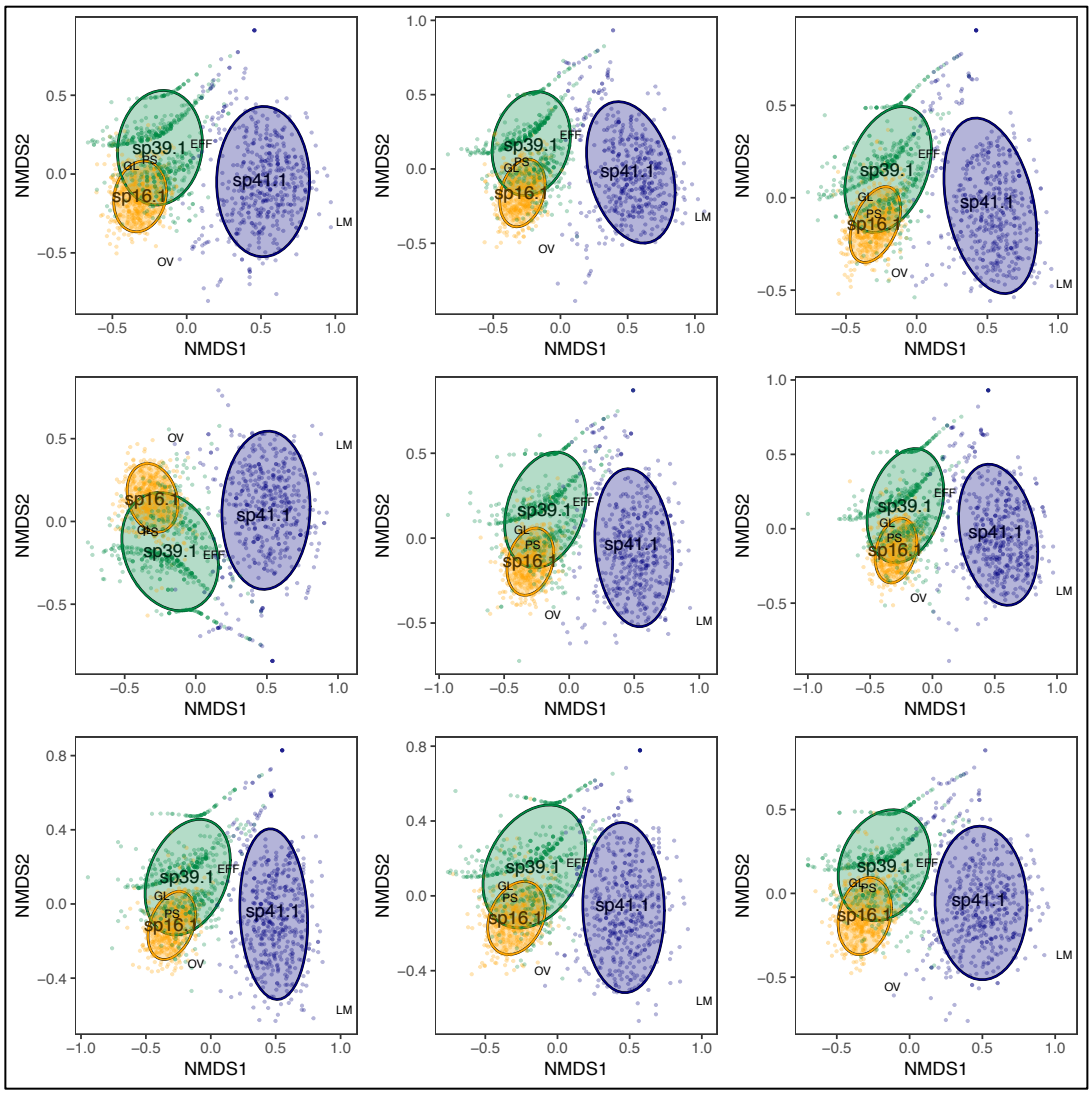


Figure 3.14 (following page): Non-metric multidimensional scaling (NMDS) ordination with elipses, which include 84% of the datapoints closest to the centroid, for the three most abundant plant hosts (with at least a total of 50,000 mm^2) and functional feeding groups present at the JARS locality. EFF is external foliage feeding, LM is leaf mining, GL is galling, and OV is oviposition.

feeding, and PH41.1 was associated with this cluster and with leaf mining. When only plant hosts with high total surface areas were included in the ordination, we see that again PH41.1 occupies a distinct region of the morphospace (Figure 3.14).

Discussion

The JARS locality within the Kaiparowits Formation is the first flora to be systematically analyzed for plant–insect associations in the Campanian Age (83.6—72.1 Ma). It captures a remarkable snapshot of a Late Cretaceous angiosperm-dominated landscape (Miller et al. 2013), as evidenced by the taxonomic diversity of plants, in which 70.0% of all plant hosts and 80.9% of all specimens at this locality are angiosperms. The Late Cretaceous was a time of large-scale shifts in insect diet from gymnosperms and ferns to angiosperms, coupled with extinction or diversification events for some herbivorous insect lineages (Labandeira 2014). In particular, the plant–insect associations at JARS illustrate specialization on host plants by Kaiparowits insects, biogeographic patterns in Campanian insect damage, and provides a strong baseline for comparisons to other Cretaceous floras and for future work in the Campanian.

JARS Damage-Type Richness and Comparisons to *Catula gettyi*

The richness of damage types for the nine most abundant plant hosts are relatively similar to one another, as seen by the overlap in confidence intervals (Figure 3.12). Only PH39.1 had a lower richness of damage types compared to PH41.1, *Quereuxia* sp. (PH12.1), and PH16.1. Based on this pattern, further sampling

may be needed to better understand the true diversities of all plant hosts, especially for small-leaved taxa. The NMDS also shows differences between several of the plant hosts, notably PH41.1, PH36.1, and Ph12.1, which also had different associated functional feeding groups. For the taxa that did have high damage type diversities and/or herbivory indices (PH41.1, *Quereuxia* sp. (PH12.1), and PH16.1) we also find interesting patterns when compared to one of the most well- sampled taxa for plant–insect associations in the fossil record, *Catula gettyi* (Figure 3.15) (Maccracken et al. in review-a).

There are no other Campanian floras systematically analyzed for insect herbivory, but quantitative and qualitative comparisons of individual JARS locality plant hosts can be made to *Catula gettyi.* In Chapter 2, I analyzed insect damage on a single plant host species, *C. gettyi*, also from the Kaiparowits Formation. Insect damage on *C. gettyi* includes 40 damage types, with five leaf mines, three damage types previously unknown in the fossil record, and an herbivory index of 2.102% for a randomly selected subsample. The *C. gettyi* herbivory index is similar to that of PH13.1 (2.00%) and *Quereuxia* sp. (PH12.1) (3.82%), and lower than the herbivory index of PH41.1 (10.68%). This means that on average, the intensity of herbivory, or the amount of surface area removed by insect herbivores, is greatest for PH41.1. However, when we look at damage-type richness and composition across the four plant hosts the differences are more striking. When rarefaction analysis is calculated for damage type richness by total sampled surface area, we see that the JARS plant hosts are not significantly different than *C. gettyi*. Interestingly, there is only moderate overlap in the suites of damage types found on the JARS plant hosts and *C.*

gettyi. Notably, there is no overlap between leaf mining, as *C. gettyi* has five leaf mine damage types (DT35, DT36, DT37, DT45, DT332), whereas PH41.1 has two (DT43, DT176), and *Quereuxia* sp. has one (DT295). This is expected, as leaf miners tend to be highly specialized to one host plant (Sinclair and Hughes 2010).

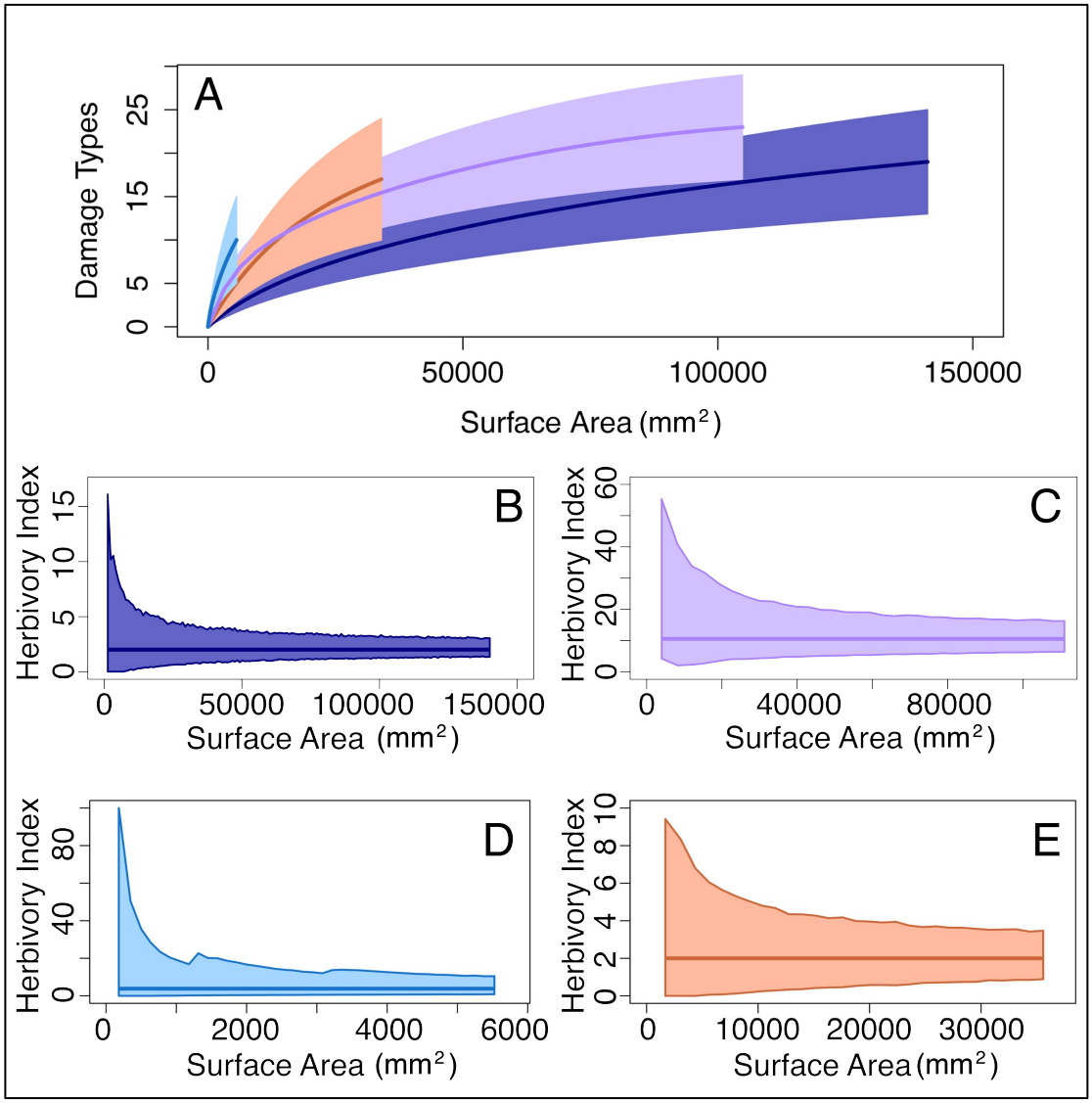


Figure 3.15: Rarefaction analysis of the damage-type richness of *Catula gettyi* (indigo) and the JARS locality plant hosts (PH) 41.1 (lilac), PH13.1 (orange), and *Quereuxia* sp. PH12.1 (blue). A, Rarefaction by surface area (X axis) and number of damage types (Y axis). B, Herbivory index of *C. gettyi* with 95% confidence interval ranges. C, Herbivory index of PH41.1 with 95% confidence interval ranges. D, Herbivory index of *Quereuxia* sp. (PH12.1) with 95% confidence interval ranges. E, Herbivory index of PH13.1 with 95% confidence interval ranges.

Host Specialization and Potential Insect Culprits

We documented a range of specialist insect damage on the plant hosts at the JARS locality, the majority of which were endophytic feeding types (Table 3.2). Functional feeding groups are established based upon both homologous and analogous mouthpart morphologies and on feeding modes (Labandeira 2019, Labandeira et al. 2007c). In general, endophytic functional feeding groups (piercing and sucking, leaf mining, galling, and oviposition) hold more clues to the identity of the insect culprit than that of ectophytic feeding groups (hole feeding, margin feeding, skeletonization, and surface feeding). This is due to greater plant host specificities (monophagous or oligophagous) among endophytic feeders (Sinclair and Hughes 2010) and their propensity towards distinctive feeding behaviors or morphologies resulting in unique signatures on leaves, such as leaf mines and scale insect impressions (ex. Hickey and Hodges 1975, Maccracken et al. in review-b, Sohn et al. 2019a, Wilf et al. 2000) compared to hole feeding insects, for example. These more distinctive damage types also often have analogues in modern plant–insect associations, which aid in the identification of the insect culprit (see Chapter 4). In contrast, ectophytic feeding groups are produced by the most common mouthpart type: insects with mandibulate mouthparts, which are represented by many different insect orders at various life stages (Labandeira 2019). In addition, the patterns of ectophytic feeding may be produced by a large number of insect species and in turn, an individual may make multiple damage types (Carvalho et al. 2014). There are exceptions to this generalization, for instance the leafcutter bee produces a distinct margin feeding damage type (DT81: a near perfect circular arc, not present at JARS)

(Sarzetti et al. 2008). However, based upon the ectophytic feeding damage types found at JARS, we cannot link any the ectophytic damage types to particular insect clades. We are able to, however, postulate about the potential identities of the endophagous insect culprits, which provides a baseline for the potential suite of herbivorous insects in the Kaiparowits Formation.

Three of the four piercing and sucking damage types (DT46, DT47, DT330) at the JARS locality are made by herbivorous insects with a stylet-like mouthpart, such as Hemiptera (true bugs) and Thysanoptera (thrips). Moreover, the piercing and sucking damage types are not associated with impression marks, indicating that the JARS piercers and suckers are free-living herbivores as opposed to hemipteran scale insects. Although we cannot narrow the insect culprit identification beyond that of a free-living Hemiptera or Thysanoptera, we understand that Hemipteroidea (the clade of Hemiptera and Thysanoptera) evolved during the Mississippian (ca. 350 Ma) (Misof et al. 2014) and had a substantial diversity by the Cretaceous (Jarzembowski 1995, Ross et al. 2000). Furthermore, the diameter of the three piercing and sucking damage types are larger in size than thrips damage, as thrips are minute (usually ≤ 1 mm in length) and it is likely that the JARS piercing and sucking was produced by hemipterans, which are larger (between 1 mm and 15 cm in length).

The three other endophytic feeding groups give clues to the identities of the damage-causing insects. First, leaf mining damage types are made by larval insects with mandibulate mouthparts and today are comprised of four orders: Lepidoptera (moths), Diptera (flies), Hymenoptera (sawflies), and Coleoptera (beetles), although moths and flies are the most common leaf miners (Csóka 2003, Hering 1951, Sinclair

and Hughes 2010). There are three leaf mining damage types at the JARS locality (DT43, DT176, DT295). The damage type DT43 is similar in morphology to nepticulid leaf mining moth mines (family Nepticulidae). Nepticulid moths are known from leaf mines of Early Cretaceous floras (Doorenweerd et al. 2015, Labandeira et al. 1994, Wahlberg et al. 2013) and are therefore likely candidates for the producers of DT43. The leaf mines DT176 and DT295 are not identifiable to clade, but are likely the work of leaf mining moths based on the size and trajectories of the mines (Donovan et al. 2014).

Second, gall makers are known from the arthropod orders: Hymenoptera (gall wasps); Diptera (gall midges); Acari (mites); and a few Hymenoptera (sawflies); Lepidoptera (moths); and Coleoptera (beetles) (Meyer 1987), as well as fungal pathogens (Akai 1950). The gall damage types at JARS are ranked as intermediate (DT32, DT34, DT194) or specialist (DT33, DT85) in host plant specialization, but identification of gall to a particular arthropod clade is not possible.

Third, oviposition of insect eggs into the tissue of a plant host is frequently encountered on *Quereuxia* sp. and PH36.1 (Figure 3.9 C). Oviposition on *Quereuxia* sp. is also reported from the Campanian of Russia and is attributed to dragonfly (Odonata) oviposition (Vasilenko 2008) (see below for an analysis of *Quereuxia* oviposition).

The NMDS ordination plot for each of the nine common plant hosts and general categories of herbivorous insect damage also demonstrates insect specialization for particular plant hosts at JARS. As mentioned above, *Quereuxia* sp. (PH12.1) is often targeted by ovipositing insects, likely belonging to the order

Odonata. PH36.1, a putative moonseed (*Menispermum*), was targeted by piercing-and-sucking insects, likely an hemipteran. PH41.1 was also targeted by leaf miners, as well as external foliage feeders that caused generalized hole and margin feeding damage.

Perhaps the most intriguing insect herbivory at JARS was targeted on PH41.1 (see Appendix E for a description of this taxa). This taxon has very large leaves on average 3176.28 mm^2, which included a moderate to high diversity of damage types (23 damage types, Figure 3.12), a 91.2% specimen damage rate, and the greatest herbivory index of any JARS plant host (10.54%). The damage types that accounted for much of the insect damaged surface area were categorized as external foliage feeding, which, although moderately diverse may have been produced by the same insect pest. Interestingly, this plant host is also found at another Kaiparowits locality, DMNH loc. 4000, although the leaves are far less damaged by insects. This, coupled with the anomalously high herbivory index at the JARS locality, implies that PH41.1 was not universally herbivorized intensely and we cannot say that it is one of the most heavily herbivorized taxa in the paleobotanical record. Instead, the data point to an outbreak of insect herbivory, a rare event in the fossil record (Labandeira 2012). A quantitative analysis of insect damage on PH41.1 across the entire Kaiparowits Formation, which is outside the scope of this chapter, is needed to test this hypothesis.

Biogeography of Odonate Oviposition

Quereuxia is a morphogenus (genus identified solely by morphology and unassignable to a plant family) of an extinct aquatic angiosperm, sometimes

preserved as a rosette of small, circular leaves or as a detached leaf (Hickey 2001). *Quereuxia* are found in a range of Late Cretaceous to Paleocene deposits (Golovneva 2000). Specimens of this morphogenus are frequently collected in the Kaiparowits Formation (Miller et al. 2013) and are found in other Laramidian formations (Crabtree 1987, Crabtree 1989, Parrish and Spicer 1988, Spicer and Parrish 1987) as well as Asian and European floras of the same age (Golovneva et al. 2008, Herman and Kvaček 2007, Kodrul et al. , Kvaček and Herman 2004).

Quereuxia of Campanian Age are especially common in the Amur region of Russia, and oviposition was extensively described on *Q. angulata* (Lesq.) Krysht. leaves from the Udurchukan locality of the Upper Kundar Formation (Vasilenko 2008). Vasilenko (2008) described multiple ichnospecies of *Paleoovoidus*, which was hypothesized to have been produced by damselfly and dragonfly oviposition. Many of the oviposition scars described by Vasilenko (2008) are lines of eggs or egg scars produced by the arcuate (fan-shaped) movement of an odonate ovipositor while the thorax was initially stationary on the leaf and the abdomen swung in broad arcs as the insect moved slightly forward (Hellmund and Hellmund 1996). Similar and abundant oviposition scars are also found on *Quereuxia* leaves from the Kaiparowits Fm., with 27.5% of the JARS *Quereuxia* specimens exhibiting oviposition damage (Figure 3.9 B,C,E). These damage types (DT100, DT101), although not in arcuate patterns, do include linear arrangements of eggs and are hypothesized to be odonate in origin. Interestingly, there were several species of aquatic and floating aquatic plants at the JARS locality, including *Cobbania* c.f. *corrugata* and *Hydropteris* sp., none of which

exhibited oviposition scars. This indicates that odonates targeted *Quereuxia*, even if there were other species of floating aquatic angiosperms available for oviposition.

Although the species of *Quereuxia* and species of insect culprits of the Kaiparowits Formation and Upper Kundar Formation are likely different, this finding supports our hypothesis that ecological associations of *Quereuxia* extend over at least two continents and several million years. Intercontinental niche conservatism of deep time plant–insect associations can provide clues into biogeography of plants and their insect herbivores. During the Campanian, North American and Asia were connected across Cretaceous Beringia (LePage et al. 2005). With hospitable environments extending into the polar regions at this time, biotic interchange across the Beringian Corridor was likely established by the Albian at 100 Ma (LePage et al. 2005). Indeed, biotic interchange across this landmass is known from the Paleocene, but Late Cretaceous interchange is less well known (Fiorillo 2008, Vavrek et al. 2014, Wolfe 1975), and this finding may be the first evidence of widespread niche conservatism between North American and Asia during the Campanian. Further research is required to study the paleobiogeographic distributions of *Quereuxia* and its oviposition associations.

Conclusions

Our results indicate that the JARS locality within the Kaiparowits Formation included a moderate diversity of plant–insect associations. When compared to the extremely well-sampled *Catula gettyi*, damage type diversities for multiple JARS

taxa were likely greater, although additional sampling would be useful for more in-depth comparisons. The JARS locality also hosted a number of specialized herbivores, which included leaf-mining moths, chewing insects, piercing-and-sucking hemipterans, and galling insects. Several taxa were also preferentially targeted by different guilds of specialist insect herbivores, which included oviposition, leaf mining, and piercing and sucking. The diversity, intensity, and specialization of the JARS locality plant–insect associations appear to be on par with the overall diversity of the Kaiparowits Formation.

Acknowledgements

Thanks to the coauthors on this chapter: I. M. Miller, G. Bate, T. Vatan, and C. C. Labandeira. We are obliged to the Denver Museum of Nature and Science's Leaf Whackers Group for preparation of the JARS fossil specimens, and to N. Neu-Yagle, K. MacKenzie, G. Rossetto, and R. Rissman for their support. The Denver Museum of Nature and Science provided financial support for collections work. Thanks to J. Shultz his ongoing mentorship; C. Mitter, D. Gruner, and C. Delwiche for their guidance; and to the undergraduate research assistants R. Bank, E. Boswell, G. Doyle, J. Kavanaugh, I. Rolfes, and S. Win. We are also grateful to K. Hamby and E. Tienens for their advice and edits. Finally, an enormous thanks to S. Schachat for her help with the analyses.

Chapter 4: A new Late Cretaceous leaf mine *Leucopteropsis spiralis* gen. et sp. nov. (Lepidoptera: Lyonetiidae) and the deep time origin of a common agricultural pest

Abstract

A new fossil leaf mine ichnogenus and species, *Leucopteropsis spiralis* gen. et sp. nov. (Lepidoptera: Lyonetiidae), from the Late Cretaceous Kaiparowits Formation (~76.6 to 74.5 Ma) in Utah, USA, is the earliest record (75.6 ± 0.18 Ma) and only reliably identified fossil of a lyonetiid leaf-mining moth, as well as one of the oldest known fossils within the Yponomeutoidea–Gracillarioidea clade. The morphology of the fossil mine is reliably associated with Cemiostominae in mine morphology and indistinguishable from mines produced by extant members of the genus *Leucoptera*, such as the mountain ash bent-wing moth, *Leucoptera malifoliella* O. Costa, 1836. This fossil provides an important Late Cretaceous (~76 Ma) calibration point for the lepidopteran phylogeny and underscores the importance of ichnofossils in the lepidopteran fossil record.

Introduction

Ichnofossils, or the trace fossil evidence of biological activity, are important for the study of organisms in deep time. In particular, trace fossils provide direct evidence of behavior and ecological associations among species, of which the body fossil record alone often lacks (Labandeira et al. 2007c). These behaviors include feeding, oviposition, nesting, burrowing, boring, locomotion, and excretion (Buatois and Mángano 2011). Ichnofossils are especially valuable for the study of organisms with relatively poor fossil records, such as insects (Labandeira 2006a, Labandeira et al. 2007c). While insects have the greatest described species diversity of any group of extant organisms (Adler and Foottit 2009, Gaston 1991, Nielsen and Mound 2000), their fossil record is sparse relative to their estimated diversity and abundance through time (Schachat et al. 2019).

Deposits of exceptional preservation, or *Lagerstätten*, on occasion provide vivid snapshots of insect faunas through time and space; however, most terrestrial fossil assemblages entirely lack insect body fossils. The fossil record of insects also is skewed by their taphonomic (fossilization) potential, which is categorized by insect inputs, such as insect size, morphology, fragility and taxonomic group, as well as external context, such as depositional environment, water depth, and energy levels (Smith 2012). In this context, many moths (Order: Lepidoptera), which have small and lightly sclerotized bodies, consequently are not well-represented in *Lagerstätten* deposits (Labandeira and Sepkoski 1993). Indeed, the diversity of fossil moths and butterflies is about half that of the predicted fossil diversity based upon their extant

diversity (Labandeira and Sepkoski 1993). Nevertheless, the fossil record of lepidopterans is bolstered by phylogenomics (Kawahara et al. 2019, Misof et al. 2014, Sohn et al. 2013) and an extensive trace fossil record (Kozlov 1988, Labandeira 1994, Sohn et al. 2012).

The most prolific insect trace fossils are the feeding traces on leaves by herbivorous insects (Labandeira et al. 2007c). Such fossilized plant–insect associations form the basis for estimates of the diversity and intensity of herbivory in ancient floras (ex. Adroit et al. 2018a, Currano et al. 2019, Donovan et al. 2018, Filho et al. 2019, Gunkel and Wappler 2015, Labandeira et al. 2002b, Maccracken and Labandeira 2020, Robledo et al. 2018, Schachat et al. 2015, Schmidt et al. 2019, Wilf et al. 2006), as well as providing first and last appearance estimates for fossil-calibrated molecular phylogenies when trace fossils are attributable to specific lineages of herbivorous insects (ex. Doorenweerd et al. 2015, Labandeira et al. 1994, Labandeira et al. 2001, Lopez-Vaamonde et al. 2006, Wappler and Ben-Dov 2008, Winkler et al. 2009a). Although identification of the insect culprit is frequently impossible due to the unparalleled diversity of insect herbivores (Nielsen and Mound 2000), coupled with convergences in herbivore mouthparts (Labandeira 2019) and in feeding behaviors (Carvalho et al. 2014), the taxonomic identification of an insect herbivore to family, genus, or species is possible for some specialized types of feeding (ex. Jud and Sohn 2016, Sarzetti et al. 2008, Wilf et al. 2000, Winkler et al. 2010). Examples include the leaf margin removal by megachilid bees (Sarzetti et al. 2008, Wedmann et al. 2009), leaf mines of a *Phytomyza* leafmining fly (Winkler et al. 2009a), agromyzid fly leaf mines (Jud and Sohn 2016), scale impression marks and

covers by diaspidid scale insects (Wappler and Ben-Dov 2008), and possible hispine beetle (*Cephaloleichnites strongi*.) damage on Cretaceous gingers (Zingiberaceae) (García-Robledo and Staines 2008, Wilf et al. 2000).

Recently, a blotch leaf mine with a distinctive frass trail was found on a fossil leaf from the Kaiparowits Formation, of Upper Cretaceous (Campanian) age, in southeastern Utah, USA. This leaf mine is structurally identical to those made by species in the genus *Leucoptera*, a clade of micro-moths that today are well known for their damage on agricultural crops (Bajec et al. 2009, Bradley and Carter 1982, Maciesiak 1999, Notley 1948, Schmitt et al. 1996). The fossil leaf mine is most similar to the mines of extant *Leucoptera*, such as the wildly polyphagous leaf miner species *L. malifoliella* O. Costa, 1836 (Bajec et al. 2009, Ellis 2018, USDA 2011). Here, we describe the leaf mine ichnofossil and discuss this ichnospecies within the phylogeny of the Lyonetiidae.

Geological Setting

The new ichnospecies was found on a fossil leaf from the Kaiparowits Formation is in the Grand Staircase-Escalante National Monument, Utah, USA (Figure 4.1). The formation is ~1,005 m thick and consists primarily of sandstone and mudstone beds derived from the Sevier Orogenic Belt immediately to the west (Beveridge et al. 2020, Roberts et al. 2005). These sediments were deposited in channel, lake, and floodplain settings on the western margin of the Western Interior Seaway coastal plain that extended from the Arctic to the Gulf of Mexico (Beveridge

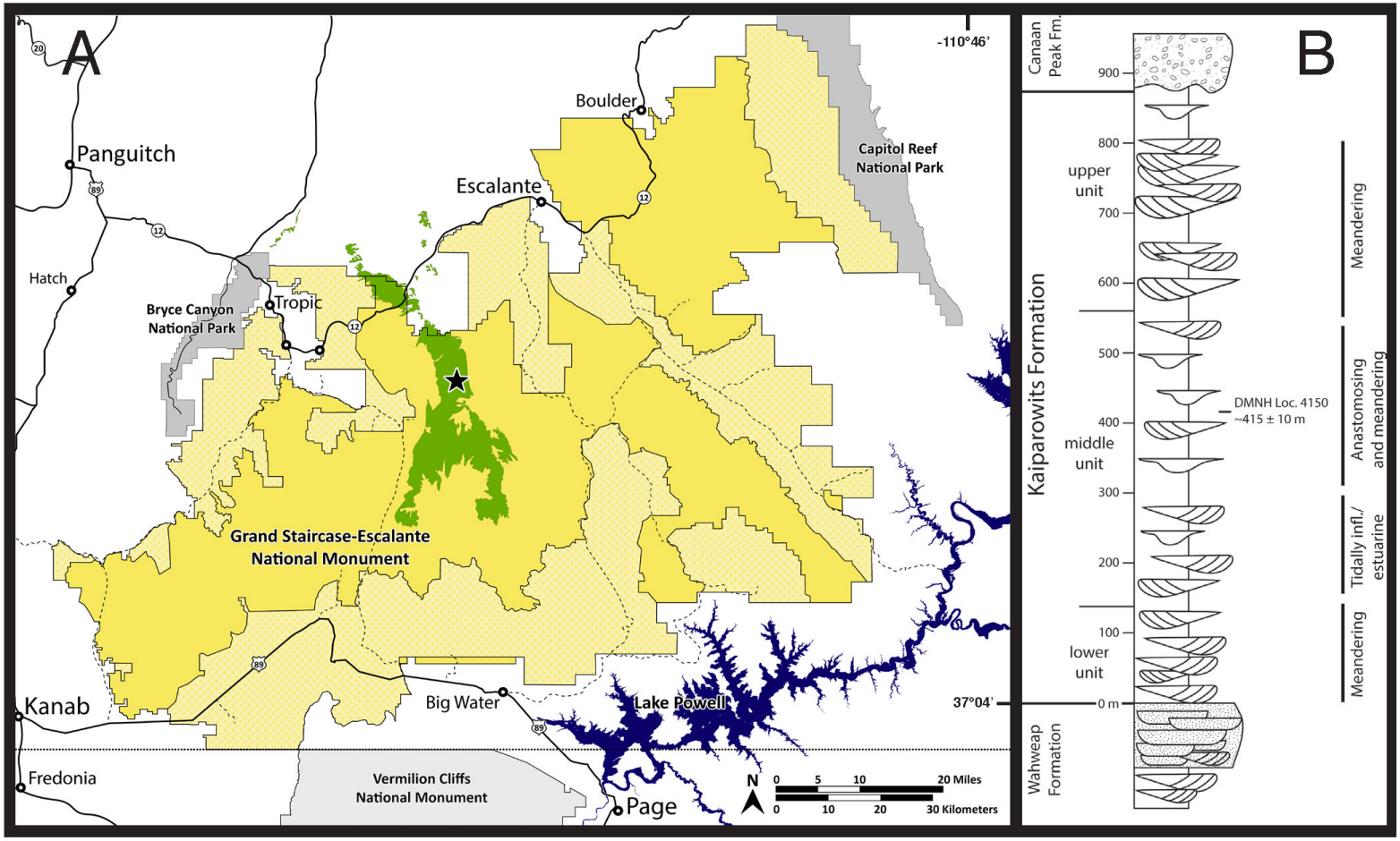


Figure 4.1: (a) Map of the Grand Staircase–Escalante National Monument in Utah, USA, with the Kaiparowits Formation outcrop shown in green. Solid yellow denotes new monument boundaries (December 2017) and former monument boundaries are stippled in light yellow. DMNH loc. 4150, the Lost Valley locality, is denoted by a star. Map adapted from Crystal et al. (2019). (b) Stratigraphic column for the Kaiparowits Formation redrawn from Roberts (2007). Stratigraphic position of DMNH loc. 4150 is indicated.

et al. 2020, Roberts et al. 2005, Roberts et al. 2013). The Kaiparowits Formation is divided into informal lower, middle, and upper units comprising ~860 m of strata (Roberts 2007) and a new formal Upper Valley Member that adds ~255 m at the top of the formation (Beveridge et al. 2020). The middle unit produces the vast majority of fossil localities, including fossil plant localities (Miller et al. 2013, Roberts 2007). Based on $^{40}Ar/^{39}Ar$ dating of volcanic ashfall beds, the age of the informal lower to upper units in the Kaiparowits Formation (the traditionally recognized ~860 m of section) is 76.49 ± 0.14 to 74.69 ± 0.18 Ma (Roberts et al. 2013). The Upper Valley Member extends the top contact to ~72.8 Ma with a confidence interval of about one million years (Beveridge et al. 2020).

The fossil floral and faunal composition, alongside evidence of depositional environments, suggests that the Kaiparowits Formation was deposited in a warm and humid palaeoclimate. Fossil leaves indicate a mean annual temperature of ~22 °C and mean annual precipitation of ~180 cm per year (Miller et al. 2013). Oxygen and carbon isotopes, and palaeoclimate modeling, suggest possible monsoonal weather patterns (Sewall and Fricke 2013) and seasonal flooding (Crystal et al. 2019). Considering both depositional and fossil evidence, the palaeo-landscape of the Kaiparowits Formation arguably was similar to that of the present-day Gulf Coast in North America and certain areas of Southeast Asia (Crystal et al. 2019, Roberts 2007).

The new ichnospecies was found on a fossil leaf collected from DMNH loc. 4150, known as the Lost Valley locality. The depositional environment and leaf preservation at DMNH loc. 4150 are described in Maccracken et al. (in review-a,

2019). Briefly, fossil leaves occur as compression–impression fossils in stacked 5–10 cm thick, fine-grained sandstone beds with minor mud partings. The depositional environment is interpreted as a medial to distal crevasse splay resulting from an event or events that infilled a perennial pond or small lake (Maccracken et al. in review-a). DMNH loc. 4150 occurs in the middle member of the Kaiparowits Formation about 415 ± 10 m above the base of the formation (Figure 4.1). Considering the stratigraphically nearest dated volcanic ash beds, using a depositional rate of 41 cm/1,000 years (Roberts et al. 2013), and assuming continuous deposition, the age of DMNH loc. 4150, and the new fossil ichnospecies, is 75.6 ± 0.18 Ma.

Materials and Methods

The discovery of the leaf mine was made while searching for evidence of insect damage on fossil leaves from DMNH loc. 4150. The leaf mine occurs on a single part-and-counterpart specimen (DMNH 47962a and DMNH 47962e). The specimen is housed in the palaeobotanical collections at the Denver Museum of Nature & Science. A Motic SMZ-161 stereoscopic microscope was used to view the fossil leaves. Detailed photographs were taken using a Canon EOS 5D Mark II camera with a Canon 65mm 1–5x macro lens. This assembly was mounted on StackShot hardware on a copy stand. Digital images were processed using Adobe Photoshop CC® (2017.01) and Zerene Stacker® focus-stacking software. Dimensions of the leaf mine were measured in Adobe Photoshop CC® (2017.01) and *ImageJ* (Schneider et al. 2012).

For the phylogenetic analysis, DNA barcodes were obtained from GENBANK (www.ncbi.nlm.nih.gov/genbank) for 15 species of extant Lyonetiidae (lyonet moths) and two out-groups of Gracillariidae (leaf blotch miner moths). Accession numbers of all these sequences are provided in Table 4.1. The collected DNA barcodes were aligned and edited using Geneious v. 11.1.4 (Biomatters Ltd.).

Table 4.1: Accession numbers and base-pair (bp) lengths for the COI sequences in GENBANK (regular font) and the BOLD system (bold font).

Family	**Genus**	**Species**	**Accession No.**	**Seq. length (bp)**
Gracillariidae	*Caloptilia*	*fidella*	JN272059.1	658
Gracillariidae	*Caloptilia*	*azaleella*	HM405768.1	653
Lyonetiidae	*Lyonetia*	*clerkella*	KX360270.1	658
Lyonetiidae	*Lyonetia*	*prunifoliella*	MG470066.1	588
Lyonetiidae	*Lyonetia*	*ledi*	KT147628.1	630
Lyonetiidae	*Lyonetia*	*candida*	MG468023.1	588
Lyonetiidae	*Leucoptera*	*lustratella*	JF853896.1	658
Lyonetiidae	*Paraleucoptera*	*albella*	KR446906.1	581
Lyonetiidae	*Paraleucoptera*	*sinuella*	HM873108.1	658
Lyonetiidae	*Perileucoptera*	*coffeella*	**LTOL915-08.COI-5P**	658
Lyonetiidae	*Leucoptera*	sp. (KLM)	MH417719.1	632
Lyonetiidae	*Leucoptera*	*malifoliella*	KF367653.1	684
Lyonetiidae	*Leucoptera*	*heringiella*	**DEEUR1010-16.COI-5P**	407
Lyonetiidae	*Leucoptera*	*laburnella*	KR941504.1	576
Lyonetiidae	*Leucoptera*	*orobi*	JF853767.1	658
Lyonetiidae	*Leucoptera*	*lathyrifoliella*	KT782401.1	658
Lyonetiidae	*Leucoptera*	*spartifoliella*	KR940230.1	588

A phylogenetic tree for the aligned DNA barcodes was constructed under the Maximum Likelihood (ML) criterion, using a default setting for RAxML-HPC Blackbox (Stamatakis 2014) through CIPRES Science Gateway website (www.phylo.org). Confidence was estimated by bootstrapping (BP), implemented in RAxML with 1000 resampling sets. The resulting trees were visualized using FigTree v.1.4.3 (Rambaut 2015), with a root at the divergence between in-groups and two species of *Caloptilia*. For comparison, the Neighbor-joining (NJ) tree was constructed

for the same DNA barcode data, using the Geneious tree builder in Geneious ver. 11.1.4. The genetic distance model was set as HKY with 'resampling tree' option (BP pseudoreplicates = 1,000).

A formal description is forthcoming and all references to this ichnogenus and species should refer to that publication.

Systematic Paleontology

Phylum Arthropoda von Siebold, 1848

Subphylum Hexapoda Latreille, 1825

Class Insecta Linnaeus, 1758

Order Lepidoptera Linnaeus, 1758

Family Lyonetiidae Stainton, 1854

Ichnogenus *Leucopteropsis* Maccracken, Sohn, Miller & Labandeira, 2019, gen. nov.

(Figure 4.2A–C)

Type ichnospecies. *Leucopteropsis spiralis* Maccracken, Sohn, Miller & Labandeira, 2019, sp. nov., by monotypy

Ichnogenus diagnosis.—Blotch mine large, circular to sub-circular in shape. Outer rim of mine thickened and dark in color. Oviposition site near center of mine on abaxial side of leaf, avoiding major leaf veins and leaf margin. Frass trail dark, continuous, thick, arcuate, and encircling in trajectory; starting near center of mine at

oviposition site; expanding in width and darkening in color as it concentrically spirals towards outer edge. Mine background light in colour, contrasting with a darker hued frass trail, and equally dark outermost rim of reaction tissue. Frass trails do not cross but do bifurcate and rejoin in their trajectories. No exit or pupation site is evident.

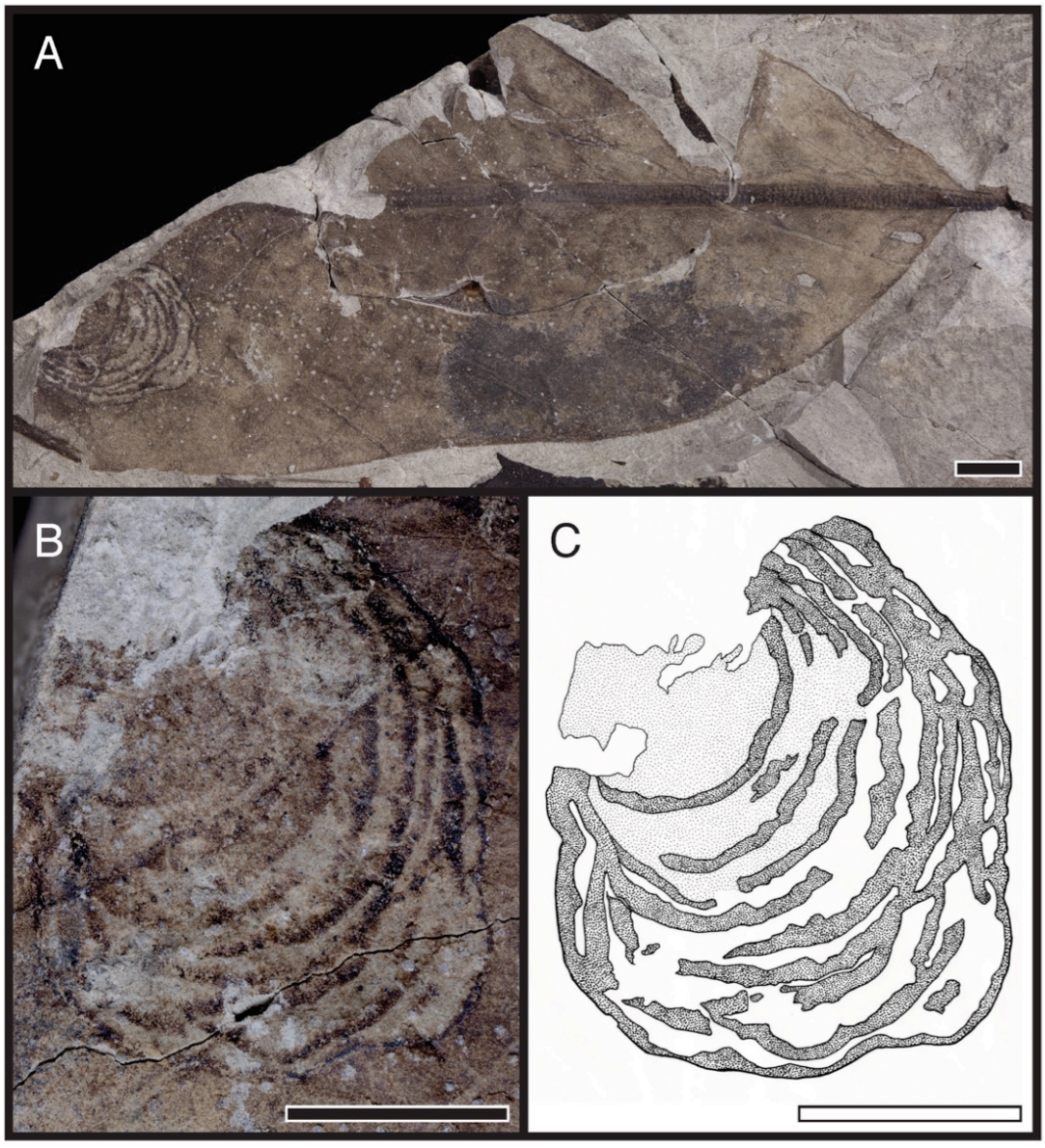


Figure 4.2: *Leucoptera* fossil leaf mine: (a) The partially broken specimen includes the newly described leaf mine. (b) A close up of the leaf mine. (c) An overlay drawing of the leaf mine.

Etymology.—The ichnofossil resembles leaf mines are produced by extant *Leucoptera malifoliella* (Lepidoptera: Lyonetiidae) leaf miners. Derivation of the ichnogenus name is from the classical Greek words *leukos*, for "white"; *pteron* for "wing"; and *ópsis* for “likeness”, or “resemblance”).

Material.—One part and counterpart specimen (DMNH 47962a and DMNH 47962e) occurs on plant morphotype KP90 (description below) from DMNH loc. 4150 located in the Upper Cretaceous Kaiparowits Formation of Utah, USA. Precise GPS locality information is available upon request.

Description.—The mine is comprised of two distinct regions: a lighter inner circle of removed tissue with relatively even shading, and an outer portion with a concentric, spiral frass trail. The surface area of the preserved leaf mine covers 97.10 mm^2 and our estimate for the full leaf mine is 105.96 mm^2; 91.6% of the mine is estimated to be present. The mine is not perfectly circular; at the widest aspect, the mine is 11.49 mm in diameter, although the fossil leaf specimen containing the mine is broken, we estimate the full diameter close to 12.30 mm. The intact side has a radius of 7.42 mm at the greatest breadth and we estimate the radius of the broken-off portion to be 4.60 mm. This makes our reconstructed mine surface area estimate fairly conservative and the surface area of the full mine could have been greater than our approximation.

As the larva moved within the leaf, it fed on internal leaf tissue and left a trail of frass that marked its precise trajectory. The movement of the larva inside the fossil leaf appears to start at the center of the mine and radiated in an arcuate trail that expanded outward with each concentric turn. The frass trails are between 0.25 mm

and 0.79 mm in width and the distance between frass trails is between 0 mm and 0.84 mm. Along the peripheral edge of the larval feeding zone is a thickened rim of reaction tissue produced by the plant in response to the herbivorized edge that is 0.16 mm to 0.73 mm in width. A pupation chamber is not present, and pupation site likely was external to the mine.

Remarks.—We circumscribe *Leucopteropsis* to any leaf mine of fossil Cemiostominae that exhibit a spirally concentric fecal trajectory. This ichnogenus is indistinguishable from blotch leaf mines produced by moths in the extant genus *Leucoptera*. In general, *Leucoptera* mines are blotches that are circular in shape, with arcuate, approximately concentric frass trails. The closest morphology to *Leucopteropsis spiralis* mines is extant mines produced by *Leucoptera*, such as those produced by *L. malifoliella*, as the frass trails of each mine are indistinguishable from one another. Consequently, we are confident that the leaf miner of *L. spiralis* belongs within the family Lyonetiidae. We erect a new genus for this mine-type because we are unable to know the morphology, and therefore the taxonomy, of the moth specifically responsible for *L. spiralis* mines, and an ichnogenus for this mine-type has not been named previously.

Ichnospecies *L. spiralis* Maccracken, Sohn, Miller & Labandeira, 2020 sp. nov.

Specific diagnosis.—Same as the generic diagnosis.

Etymology.– The specific name refers to the spiral pattern of the frass within the blotch mine; from classical Greek, derived from *speira*, meaning “spiral”).

Type specimens.—Designated herein: holotype DMNH 47962a and DMNH 47962e, part and counterpart (Figure 4.2A–C).

Damage type.—DT178. The *Leucopteropsis spiralis* mine is included in the amended version of the *Guide to Insect (and Other) Damage Types on Compressed Plant Fossils* (Labandeira et al. 2007c) as damage type DT178.

Differential Diagnosis.—A blotch mine, identified as *Tischeria* sp. (Specimen no. IU15808-7545, Mine type KLm14) from the Maastrichtian of Tennessee (Ripley Formation) was illustrated by Stephenson (1992) (Sohn et al. 2012, Stephenson 1992) and the damage type was described as a medium to large blotch mine generally on the primary vein, with thickened outer walls and frass absent. The accompanying illustration of mine type KLm14 is similar to the *Leucopteropsis* mine, but close examination of the specimen revealed features inconsistent with a *Leucopteropsis* mine (Supplementary Figure 4.1 A,B in Appendix D). A second blotch leaf mine from the Miocene San José Formation of Argentina was compared to extant *Leucoptera malifoliella* moths (Specimen no. CTES-IC 176, new damage type) (Robledo et al. 2018). The mine is circular, ca. 4 mm in diameter, with a smaller, circular patch of frass ca. 1.5 mm in diameter and bordered by a thick fringe of reaction tissue. As noted in the original paper, the frass does not form a spiral pattern within the mine, a characteristic of *Leucoptera* mines (Ellis 2018, Robledo et al. 2018, USDA 2011). We posit that this mine is more similar in morphology, although not necessarily related to, leaf mines made by the gracillariid moth species *Phyllonorycter issikii* Kumata, 1963 (Supplementary Figure 4.1 C, D).

Host Plant.—The *Leucopteropsis spiralis* mine occurs on a partial angiosperm leaf of unknown affinity. We provide a brief description of the host plant here; a full description of the leaf architecture of the host taxon is provided in the Supplementary Material (Appendix D). The taxon is provisionally designated as KP90 in the Kaiparowits Formation morphotype series. KP90 is pinnate, with somewhat irregularly spaced brochidodromous secondary venation, interspersed with frequent intersecondary veins. The primary vein is notably thicker than the secondary and higher order veins. The tertiary venation is mixed alternate and opposite percurrent, and quaternary venation appear irregular reticulate. KP90 is untoothed and exhibits a somewhat undulating margin; it is typically oblong and slightly asymmetrical in shape. The petiole is thick compared to the leaf area indicating a high leaf mass per area (Royer et al. 2007). Overall, many specimens of KP90 are generally well preserved and exhibit 4^{th} and 5^{th} order venation.

We have identified 67 specimens of KP90 from DMNH loc. 4150. While a comprehensive examination of all plant localities in the Kaiparowits Formation has yet to be completed, KP90 appears minimally in three other localities within the formation. Although there is presently only one known instance of the *Leucopteropsis* mine, KP90 is heavily herbivorized and hosts a diverse suit of insect herbivore traces. Only twenty of the leaf specimens (29.85%) had no apparent damage while 47 specimens (70.15%) exhibited between one and four damage types. Among all KP90 specimens, there were a total of 25 damage types, grouped into seven functional feeding groups: margin feeding, hole feeding, skeletonization, surface feeding, piercing and sucking, mining, and galling (see Labandeira et al. 2007c for a

description of the damage spectra). Notably, there are other blotch-mine damage types found on KP90, which differ in shape and often lack frass as compared to the *L. spiralis* mine. The leaf specimen housing the *L. spiralis* mine (DMNH 47962a and DMNH 47962e) also contains margin feeding (DT15) and two types of hole feeding (DT01, DT02) (Labandeira et al. 2007c).

Results and Discussion

Evidence of lepidopterans during the Cretaceous, including the *Leucopteropsis spiralis* leaf mine described herein, is crucial to understand the diversity and evolution of Lepidoptera. Lepidopteran body fossils and ichnofossils are rare in Mesozoic deposits and are often difficult to identify to specific taxonomic groups (Schachat and Gibbs 2016, Sohn et al. 2015). The earliest known lepidopteran fossils are wing scales recovered from latest Triassic of Germany (ca. 212 Ma), and include scales of a glossatan moth (van Eldijk et al. 2018). Following this occurrence, the stem group lepidopteran *Archaeolepis mane* Whalley has been identified from the Lower Jurassic (ca. 195 Ma) of England (Sohn et al. 2015, Whalley 1986, Whalley 1985). While these body-fossil discoveries clearly indicate a Jurassic lepidopteran radiation, the diversity and abundance of lepidopteran specimens remain low throughout the Mesozoic Era (Zhang et al. 2013). A survey of lepidopteran fossil specimens from the Jurassic and Cretaceous Epochs found a total of 177 specimens (100 body fossils, 77 ichnofossils), which accounts for approximately 3% of all identified lepidopteran fossil specimens (Sohn et al. 2015). The discovery and description of *Leucopteropsis spiralis* contributes to that short list.

Identity of the leaf miner

The morphology of leaf-mines often lacks phylogenetic characters that can be ranked above the species-level. Despite their usefulness for identification of mine makers (Jud and Sohn 2016, Winkler et al. 2009b), this issue has led to serious concerns about identifications of lepidopteran leaf-mine fossils based on extant analogs (Grimaldi and Engel 2005). Indeed, convergence in two major mine features, overall trajectories and frass patterns, is commonly found among multiple lepidopteran genera of higher taxonomic groups (Hering 1951). However, as an exception, some leaf miners within the lyonetiid subfamily Cemiostominae produce distinctive blotch mines that are unique and not found in other leaf mining clades (Dugdale et al. 1998). The mine maker of the leaf fossil in the present study is reliably identified as Cemiostominae, based on the characteristics described below.

Larvae of Cemiostominae are miners in the leaves and bark of host plants and they pupate in a fusiform, silken cocoon outside of the leaf mine (Dugdale et al. 1998). Within the Lyonetiidae, the larvae of subfamily Cemiostominae principally produce blotch or linear-blotch mines that differ structurally from the typically narrow galleries of leaf-mines created by larvae in the subfamily Lyonetiinae (Dugdale et al. 1998). However, this distinction is not obvious, as some lyonetiids, e.g. *Lyonetia prunifoliella*, produce linear-blotch mines similar to Cemiostominae (Hering 1951). *Phyllobrostis*, which are leaf miners closely related to *Lyonetia* (Sohn 2013, Sohn et al. 2013), produce mines of dark blotches whose upper epidermis is consumed and deposited as larval fecal pellets (Mey 2006). However, the trajectory of this frass is serpentine and unlike that of *L. spiralis*.

Blotch mines with a concentric arrangement of frass rings that branch and rejoin are exclusively found in Cemiostominae (Mey 1994). Such a pattern is formed by deposition of frass on the underside of the upper epidermis of the host-plant foliage. These leaf mines can be found only in a few species of *Leucoptera* (Figure 4.3). In particular, the mines of *Leucoptera malifoliella* are most similar to the fossil leaf mine described herein (Figure 4.3A). While a small number of other taxa form leaf mines that superficially resemble those of Cemiostominae, none of these taxa fit all the characteristics of the leaf mines discussed here. Among all lepidopteran groups, leaf-mines of Tischeriidae may also exhibit a multiple-layered, concentric pattern that originated from progressive damage on foliar tissues by the larvae (Hering 1951) (Figure 4.3B). However, tischeriid leaf mines differ from those of *Leucoptera* by the absence of frass, as the larvae expel fecal pellets outside the leaf mines. Some species of Bucculatricidae also produce leaf-mines that often exhibit a frass pattern of concentric rings; however, these mines include both a linear segment in addition to a small blotch segment (Figure 4.3C). Some pathogenic marks on plant leaves made by ascomycotan epiphyllous fungi may also show concentric patterns, similar to *Leucoptera* leaf-mines (Figure 4.3D), but these necroses originate either as series of concentrically arrayed rings, circularly arranged pycnidia, or similar fructifications in one or multiple rings. Most common are the damage types DT66 (Xiao et al. in review), similar to Maple Tar Spot Disease; DT154 (Currano et al. 2008), resembling a leaf spot necrosis; and DT334 (Donovan et al. 2018), a different leaf spot necrosis. However, the circular patterns of fungal necroses are significantly different from the *Leucopteropsis* leaf mine. Overall, the frass patterns of the mine

described on the Kaiparowits fossil leaf morphotype KP90 (DMNH 47962a and DMNH 47962e) are indistinguishable to those of *Leucoptera* leaf-mines.

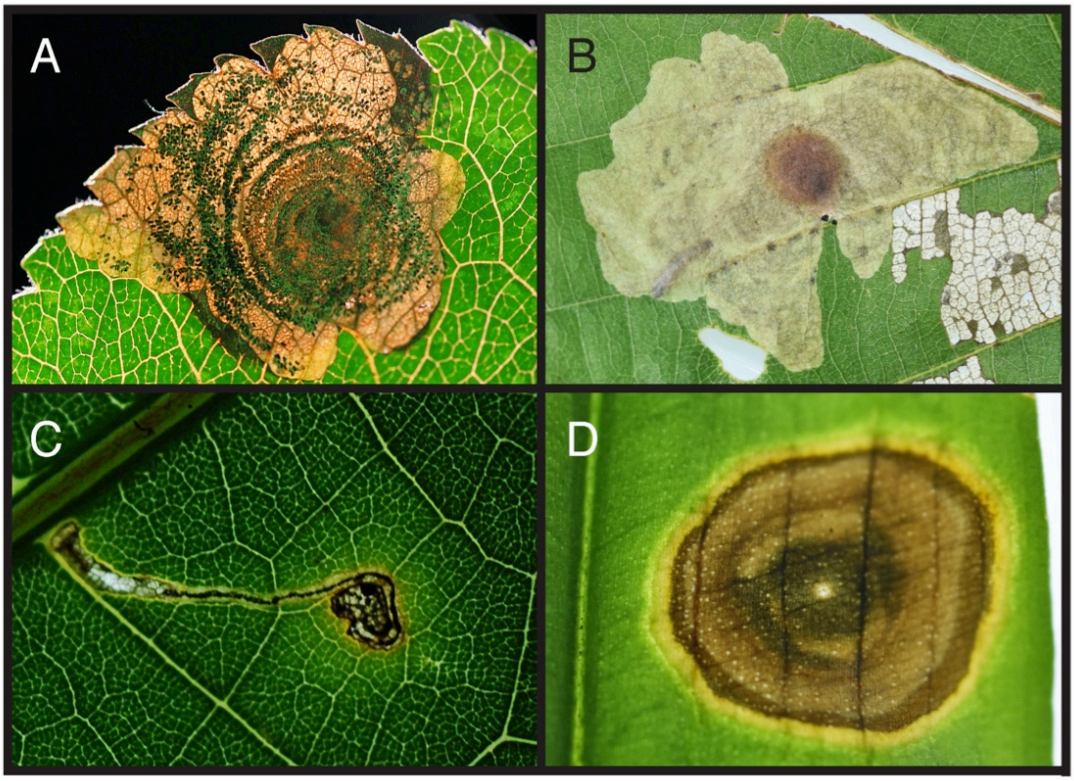


Figure 4.3: Foliar mines and a pathogen with a concentric, multi-layered pattern. (a) Leaf-mine of *Leucoptera scitella* Zeller on *Malus* sp. (Rosaceae). (Photo by György Csóka.) (b) Leaf-mine of *Bucculatrix firmianella* Kuroko on *Firmiana simplex* (L.) W. F. Wight (Malvaceae). (Rearing no. K-557.) (c) A maturing leaf-mine of *Tischeria* sp. on *Quercus mongolica* Fisch. ex Ledeb. (Fagaceae). (Rearing no. K-605.) (d) Phytopathogenic leaf blight spot on *Commelina communis* L. (Commelinaceae).

Phylogeny of the Yponomeutoidea–Gracillarioidea Group

Our fossil represents the second earliest record of the monophyletic Yponomeutoidea–Gracillarioidea (YG) group. The earliest fossil records of the group are *Phyllocnistis* leaf mines on fossilized leaves from the Early Cretaceous Dakota Formation (Davis 1994, Labandeira et al. 1994) at ca. 100–105 Ma. Although linear-

blotch mines are extremely common among leaf-mining lepidopterans (Grimaldi and Engel 2005), their phyllocnistine identity has been confirmed by Davis (1994) and Lopez-Vaamonde et al. (2006).

The *Leucopteropsis* leaf-mine fossil described in this paper can be used as the reliable fossil calibration point for the subfamily Cemiostomiae within the YG group and consequently is an indicator for the antiquity of the most diverse lepidopteran group, Ditrysia. If the family Lyonetiidae is indeed monophyletic, *Leucopteropsis spiralis* also is an important calibration point for the moth family. However, for use of fossil *Leucopteropsis* as a calibration point within the YG group, the systematic position of the Cemiostominae must be better understood. The systematic relationships of Lyonetiidae and its putative subfamily, Cemiostominae, may not be straightforward because of two current issues. First is the absence of a robust phylogeny for Lyonetiidae and its relationship to other YG clades. Second, there is limited knowledge regarding detailed mine morphology of lepidopteran leaf-mining clades.

The systematic position of Lyonetiidae remains uncertain, despite recent progress in lepidopteran phylogeny. There is broad consensus that Lyonetiidae belongs to a monophyletic clade within Yponomeutoidea and Gracillarioidea (Kawahara and Breinholt 2014, Regier et al. 2015, Sohn 2013, Sohn et al. 2013). However, the monophyly of Lyonetiidae has not been firmly established to date. The family currently includes two subfamilies, Lyonetiinae and Cemiostominae, and several genera whose subfamily affiliation remains undetermined. Two leaf-mining microlepidopteran groups, Bucculatricidae and Bedellidae, have sometimes been

treated as subfamily-level groups within Lyonetiidae (see a complete review in Baryshnikova 1999); however, the current consensus is that these two lineages belong to separate families (Kawahara et al. 2011, Sohn et al. 2013, van Nieukerken et al. 2011) (Figure 4.4).

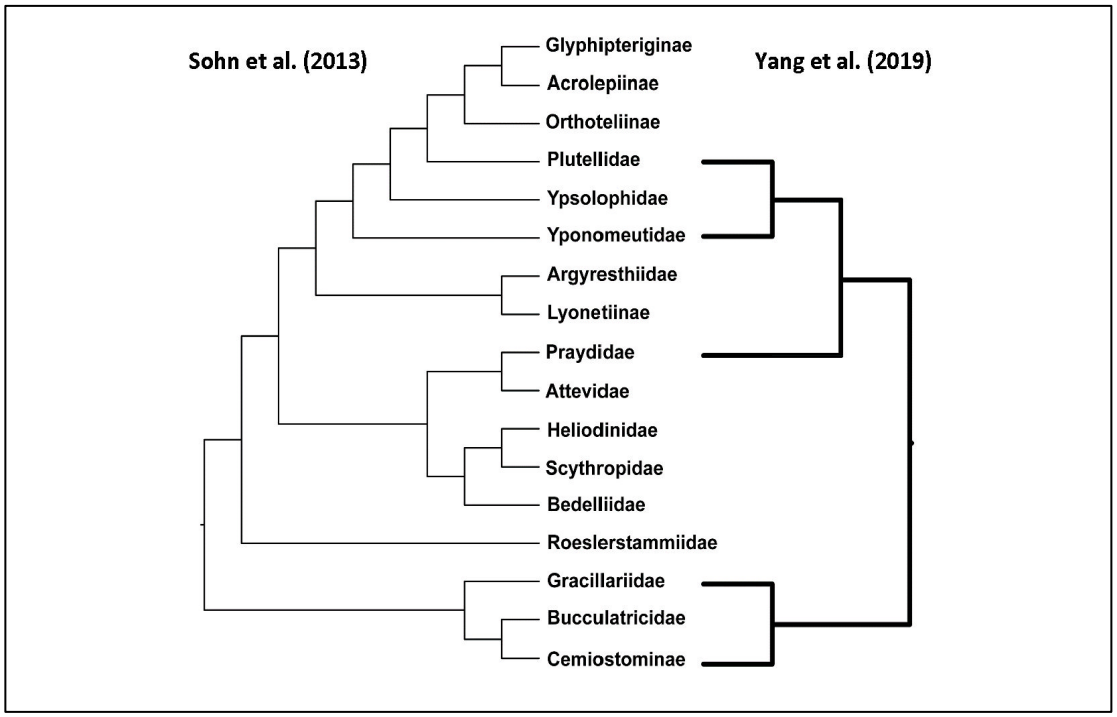


Figure 4.4: A working hypotheses as of mid 2020 of the phylogeny of Yponomeutoidea–Gracillarioidea group. At the left is Sohn et al. (2013) and at the right is Yang et al. (2019). Modified from original sources.

The location of Lyonetiinae and Cemiostominnae within the larger Yponomeutoidea and Gracillarioidea is currently debated. Sohn et al. (2013) found that Lyonetiinae and Cemiostominae were placed, respectively, in the more distantly related clades of Yponomeutoidea and Gracillarioidea (Figure 4.4). In their phylogeny, only Lyonetiinae were placed within Yponomeutoidea as a basal lineage, while Cemiostominae were grouped with Gracillariidae and Bucculatricidae. These

relationships were, however, weakly supported or otherwise unstable. Interestingly, a molecular study (Yang et al. 2019) based on mitochondrial genomes resulted in grossly similar relationships (Figure 4.4), although the analysis lacked several important groups of Yponomeutoidea and Gracillarioidea in the analysis. Morphological characteristics also support the non-monophyly of Lyonetiidae, as Lyonetiinae and Cemiostominae show two major differences: the relative length of antenna to forewing and the presence/absence of spiniform setae on the abdominal terga. For these reasons, we believe that Cemiostominae are closer to Gracillariidae than to Yponomeutoidea, and likely represents one of the three basal lineages to the entire YG clade.

Cemiostominae currently includes about 120 species in six genera (Sohn 2020). The majority (ca. 75%) of these species currently belong to *Leucoptera*, but a comprehensive generic revision may reveal several new genera. Host plants are documented for about 50% of Cemiostominae and data on their mine morphology is often lacking (Bradley and Carter 1982). Furthermore, the astonishingly high numbers of host plant species for each nominal leaf-miner species suggest that several species of *Leucoptera* are likely suites of cryptic species. This anomalously high level of host-plant breadth is suspect, given that the majority of leaf miners are monophagous (Prins et al. 2019). One example of this suspect polyphagy is the more than 25 host-plant species that are associated with the agricultural pest *L. malifoliella* Costa (Bajec et al. 2009, Ellis 2018, USDA 2011).

Within the genus *Leucoptera*, not all members produce blotch mines with concentric frass layers. Searching available online libraries (e.g.

www.leafmines.co.uk; www.ukflymines.co.uk) and the entomological and agricultural literature (e.g. Csóka 2003, Hering 1951) of insect leaf-mines, we collected data on mine morphologies from 16 species of *Leucoptera* and found that blotch mines with concentric rings of frass occurred minimally on five species: *L. heringiella* Toll, *L. laburnella* Stainton, *L. lotella* Stainton, *L. malifoliella* Costa, and *L. onobrychidella* Klimesch. Frass patterns in some mines of *Leucoptera coronillae* Hering can appear concentric but in later stages, this pattern becomes disarrayed. Based on the divisions of *Leucoptera* proposed by Mey (1994), the above species are scattered in four species-groups. A COI-based phylogeny of 15 lyonetiids included three species whose larvae make blotch mines with a concentrically-ringed frass pattern. In the resulting Neighbor-Joining and Maximum Likelihood trees, these three species did not form a monophyletic group (Figure 4.5). In our COI phylogeny, the *lustratella*-group in Mey's (1994) divisions was represented by only one species, *Leucoptera lustratella*, whereas the group from other analyses includes at least two species that produce blotch mines with concentric frass layers. Consequently, we conclude that the blotch mine with concentric rings of frass is very likely an ancestral form of mine type in the *Leucoptera* lineage. Nevertheless, it also is possible that the blotch mines with concentric frass rings have evolved multiple times independently. A denser sampling of the cemiostomine leaf-mines may help evaluate these two hypotheses. Because of the lack of a reliable phylogeny and a dense species-level tree for Lyonetiidae, divergence time estimation currently is not feasible. Our fossil

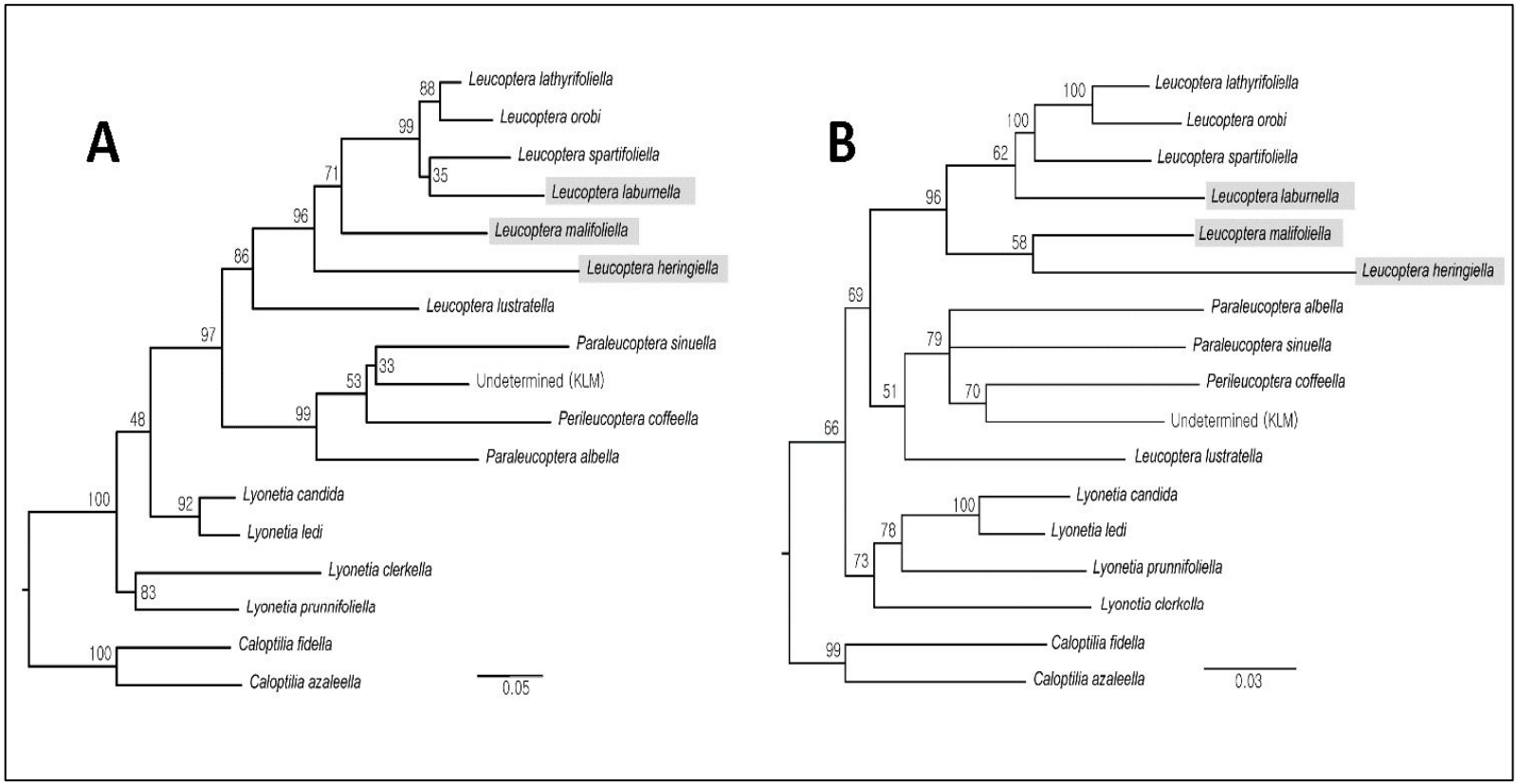


Figure 4.5: COI phylogeny of 15 lyonetiid and two gracillariid species. A: Maximum Likelihood Tree, B: Neighbor-joining tree. Numbers on nodes indicate percent bootstrapping support. Terminal label in the gray box represents the species producing blotch mines with a concentric, multi-layered frass pattern.

specimen of *Leucopteropsis* will become increasingly useful as a calibration point for the subfamily Cemiostominae once the uncertainty involving the gap between fossil age and actual divergence time is properly modeled.

Conclusions

The fossil leaf mine in the new ichnogenus and ichnospecies, *Leucopteropsis spiralis* (Lepidoptera: Lyonetiidea), from the Late Cretaceous Kaiparowits Formation (type locality age ca. 75.6 Ma) is herein described. The leaf-mining moth responsible for *L. spiralis* likely is an early member of the extant genus *Leucoptera,* a common agricultural pest genus. This trace fossil documents the earliest record of a cemiostomine leaf-mining moth, as well as the second oldest record of the Yponomeutoidea–Gracillarioidea clade. Despite the need for further phylogenetic work for the Lepidoptera, particularly the placement of the family Lyonetiidae and the subfamily Cemiostominae within the larger Yponomeutoidea–Gracillarioidea clade, this fossil provides an important Late Cretaceous calibration point for the age of the Yponomeutoidea–Gracillarioidea group.

Acknowledgments

We thank J. Shultz, D. Gruner, C. Delwiche, and C. Mitter for their guidance and support. We are grateful to the Denver Museum of Nature & Science's (DMNS) Leaf Whackers for preparation of the Kaiparowits fossil specimens; K. MacKenzie,

G. Rossetto, and N. Neu-Yagle for their assistance in the collections; and J. Sertich for his leadership of the Kaiparowits fieldwork. DMNS provided financial support for the collections visit, R. Rissman and W. Rissman-Miller provided lodging and support, and The University of Maryland at College Park and the National Museum of Natural History provided the stipend for S. A. Maccracken. The second author (JCS) was supported by the 'Research Under Protection' subprogram of the Individual Research program on Basic Science and Engineering funded by the National Research Foundation of Korea (NRF-2017R1D1A2B05028793). Thanks go to M. Robledo for his assistance with the differential diagnosis and D. Davis, R. Eckert, P. Coffey, R. Gott, and C. Taylor for helping with the identification of the leaf mine. We are grateful to G. Motz and H. Wang for the loan of supplementary fossil materials. Finally, many thanks to the anonymous reviewers and editorial team. This is contribution 391 of the Evolution of Terrestrial Ecosystems at the National Museum of Natural History, in Washington, D.C.

Chapter 5: Late Cretaceous domatia reveal the antiquity of plant–mite mutualisms

Abstract

Mite houses, or acarodomatia, are found on the leaves of over 2,000 living species of flowering plants today. These structures facilitate tri-trophic interactions between the host plant, its fungi or herbivore adversaries, and fungivorous or predaceous mites by providing shelter for the mite consumers. Previously, the oldest acarodomatia were described on a Cenozoic Era fossil leaf dating to 49 million years in age. Here, we report the first occurrence of Mesozoic Era acarodomatia in the fossil record from leaves discovered in the Late Cretaceous Kaiparowits Formation (76.6–74.5 Ma) in southern Utah, USA. This discovery extends the origin of acarodomatia by >25 million years, and the antiquity of this plant–mite mutualism provides important constraints for the evolutionary history of acarodomatia on angiosperms.

Background

Mutualisms – cooperative associations among species – were key in the ecological ascendency of flowering plants (Eriksson et al. 2000, Grimaldi 1999). Pollination and seed dispersal, the two most common plant–animal mutualisms, are

widely recorded in modern and fossil communities. However, mutualisms between angiosperms and mites are less well known, despite the prominence of these interactions in modern ecosystems. Acarodomatia, or mite domiciles, located on the undersides of leaves, are thought to be the third most common plant–animal mutualism on earth today (Walter 2017) and likely contributed to the rise of flowering plants.

Acarodomatia are pouches, pits, invaginations, or hair tufts located on the undersides of leaves at the axils of major vein branches (Nishida et al. 2006, O'Dowd and Willson 1989, 1991, Romero and Benson 2005, Walter 1996) (Figure 5.1). Inhabiting these minute structures are fungivorous or predaceous mites that provide protection to the host plant from fungi or herbivorous mites in exchange for refuge from other predators. At least 27 mite families in the superorders Acariformes and Parasitiformes (Karban et al. 1995, Pemberton and Turner 1989, Walter and O'Dowd 1992) are known to occupy acarodomatia (O'Dowd and Willson 1991). In particular, the shelter provided by the leaf is important for molting and oviposition for mutualistic mites, which otherwise would face desiccation or predation without the acarodomatia (Walter and Proctor 1999). This mutualism is facultative for both protected plants and beneficial mites, with no known specialization occurring between plant and mite species (Pemberton and Turner 1989). The generalized nature of this mutualism makes tracking the evolutionary history of acarodomatia particularly difficult, as compared to other tightly coevolved associations through time, such as certain specialist pollinators and their host plants (Winkler et al. 2009a).

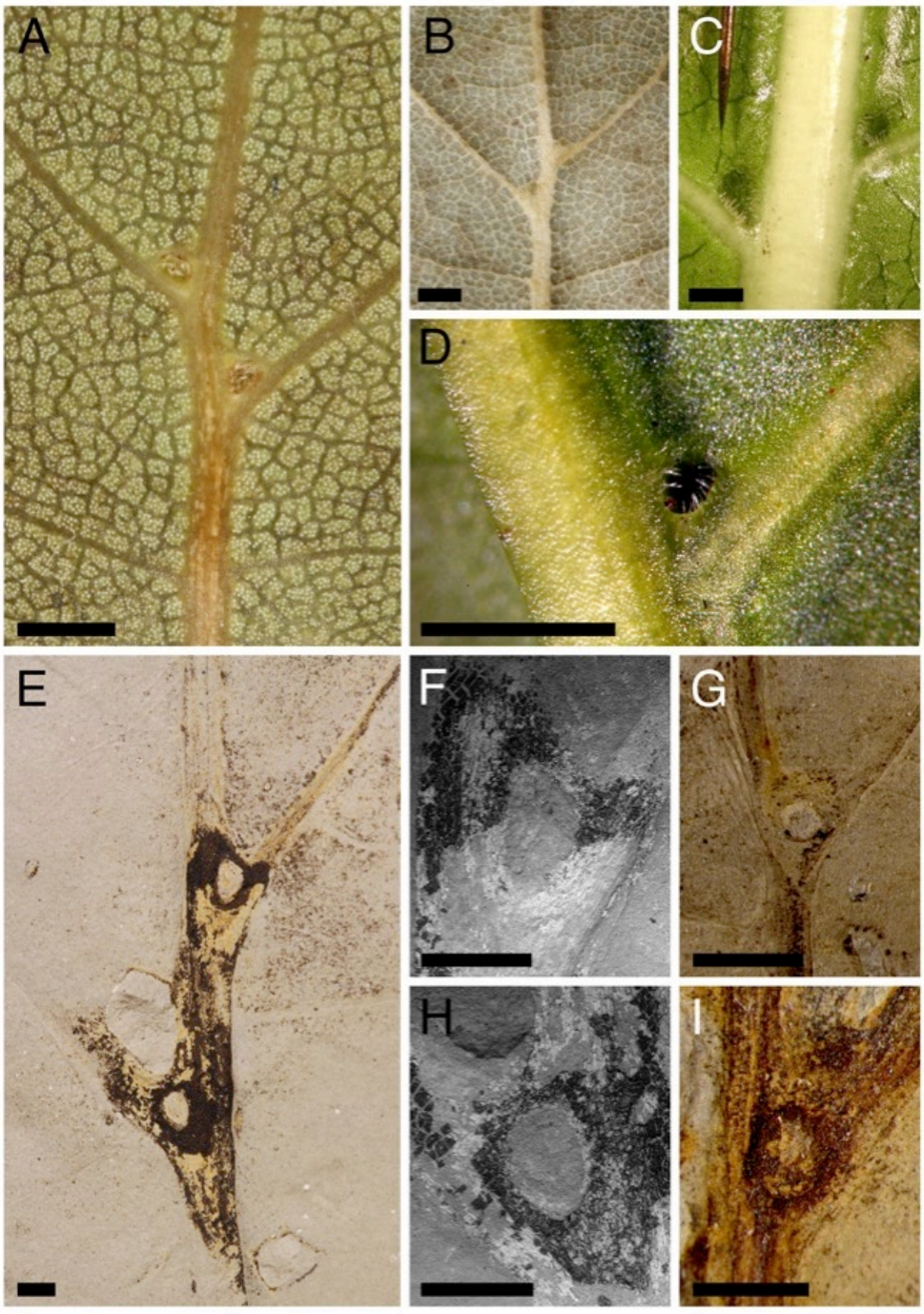


Figure 5.1: Fossil acarodomatia from the Kaiparowits Formation, UT, USA, and modern acarodomatia for comparison. (a, b) Two modern pouch acarodomatia on *Cinnamomum camphora* (L.) J. Presl. (Lauraceae), shown in the abaxial (a) and adaxial (b) orientation, (c) two modern pit acarodomatia on *Gardenia taitensis* (DC) de Candolle (Rubiaceae), photograph by S. Zona, (d) modern pit acarodomatium on *Coffea arabica* (L.) Juss. (Rubiaceae), photograph by G. Romero, (e) two fossil (EPI.45456), (f, h) SEM images of acarodomatia from (d) (EPI.45456), (g) fossil acarodomatium (EPI.40928) and (i) fossil acarodomatium dome (EPI.45427). Scale bars, 1.0 mm.

Acarodomatia presently are found exclusively on dicotyledonous angiosperms, especially woody arborescent species (Farmer 2014, Walter and Proctor 1999), with the exception of a single, unverified report of acarodomatia in the rolled leaf margins of one monocotyledonous angiosperm species (Burkill 1939). Acarodomatia are found on over 2,000 living species and 80 families – ca. 28% of dicotyledonous families (Brouwer and Clifford 1990, Pemberton and Turner 1989, Walter 2017) – of geographically widespread and taxonomically disparate angiosperms [5]. Plants have evolved acarodomatia multiple times, although the number of convergent evolutionary events is unknown (O'Dowd and Willson 1991). The percentage of trees with acarodomatia is greater than 15% in tropical forests (Brouwer and Clifford 1990, O'Dowd and Willson 1989, 1991) and range from 40% to 70% in temperate regions (O'Dowd and Pemberton 1994, 1998, Willson 1991). Despite the ecological prominence of modern acarodomatia, the fossil record of acarodomatia is sporadic and poorly understood.

The unknown timing of origination and number of convergent evolutionary events, combined with widespread presence of acarodomatia among living woody dicotyledons and generalized nature of the association between mites and angiosperms, makes the fossil record of acarodomatia essential toward understanding the evolutionary history of this mutualism. Here, we describe fossil acarodomatia from the Upper Cretaceous Kaiparowits Formation, Utah, USA, which is the earliest documented occurrence of acarodomatia to date.

Materials and Methods

Specimens were excavated from DMNH localities 3725 in 2009 and DMNH 4000 in 2010. These specimens currently are housed at the Denver Museum of Nature & Science (DMNS) in Denver, Colorado, USA. The leaves occur as compression-impression fossils on mudstone, siltstone, and fine-grained sandstone matrices (Locatelli et al. 2017) (see Supplementary Material in Appendix E for a detailed methodology). We used a Motic SMZ-161 steroscopic microscope to view the fossil leaves. Detailed photographs were taken with a Canon EOS 50D camera housing a Canon EF-D 60mm f/2.8 macro lens and an Olympus DP25 camera attached to an Olympus SZX12 microscope. Images were edited using Adobe *Photoshop CC* (19.1.3). For Scanning Electron Microscopy (SEM) images, we placed the fossil specimens in a low-temperature oven for 20 hours and used a Carl Zeiss EVO MA15 scanning electron microscope with a LAB6 electron source.

Results

Thirteen examples of the same type of acarodomatia were found on ten fossil leaf specimens from two localities of the Kaiparowits Formation (76.6–74.5 Ma), Utah, USA (Figure 5.1 E-I). Identification of acarodomatia of the Kaiparowits Formation is based on the location, size, and morphology of pore-like surface structures. The acarodomatia are located in primary-to-secondary and secondary-to-secondary vein axils and are embedded within vein tissue. These acarodomatia are classified as pouch acarodomatia, which comprise a cavity with a pore-like opening

on the abaxial side of the leaf (Figure 5.1 A, E-H) and a dome of foliar tissue on the adaxial side of the leaf (Figure 5.1I) (Jacobs 1966, O'Dowd and Willson 1989). This acarodomatium type generally is embedded within the vein tissue, as opposed to pit acarodomatia that generally occur in laminar tissues (Figure 5.1 C, D). There is substantial variation in acarodomatia classification schemes, but these fossil acarodomatia are morphologically similar to pouch domatia found on *Cinnamomum camphora* (L.) J. Presl. (Lauraceae) (Figure 5.1 A).

The pores of the fossil acarodomatia are circular to rounded-triangular in shape. They are between 0.82 and 1.18 mm along the longest dimension, 0.71 and 1.06 mm in diameter along the shortest dimension, and cover an average of 1.02 mm^2. These dimensions are consistent with modern pit and pouch acarodomatia, which are generally between ca. 0.5–3.0 mm in diameter (English-Loeb and Norton 2006). Additionally, the fossil acarodomatia are distinct from holes associated with herbivory because the structures exhibit smooth edges around the pore that lack plant reaction tissue, and are distinct from extrafloral nectaries, which tend to be bulbous and rarely occur in mid-laminar vein axils (Marazzi et al. 2013). All data and lines of evidence indicate that these foliar features are acarodomatia.

The fossil acarodomatia occur sporadically, as they are not present at every major vein juncture on the fossil leaves. At most, we observed three acarodomatia per fossil leaf. However, most of the fossil leaf specimens examined are fragmentary, and the number of acarodomatia per fossil leaf may be greater. Ten of the 41 fossil leaf specimens (24%) from the acarodomatia-bearing plant taxon exhibiting acarodomatia display evidence of at least one acarodomatium.

The identity of the fossil leaf species remains unresolved. The very large size of this leaf taxon (exceeding 30 cm in length and 25 cm in width) likely led to pre- and post-depositional foliar fragmentation. Consequently, complete fossil leaves of this taxon have not been recovered. Without exception, all known specimens of this fossil leaf have intense hole and margin feeding insect damage. In particular, the hole feeding is occasionally so extensive that up to 80% of the lamina was consumed, which further obfuscates taxonomic identification. This hole feeding appears to be unrelated to the plant–mite mutualism involving acarodomatia; mites are an order of magnitude smaller than the average insect pest and likely outside the scope of a predaceous interaction. The vein fabric of this fossil leaf – pinnate primary venation, brochidodromous secondary venation, alternate percurrent tertiary venation, and a thick, coalified, and thus likely woody petiole – and overall size of the specimens indicate it is a woody dicotyledonous angiosperm (Hickey 1971) (Figure 5.2). A morphological description of the taxon, including photos, is provided in the Supplementary Material (Appendix E).

Discussion

Distribution of fossil and modern acarodomatia

There are nine occurrences of domatia from the fossil record (Table 5.1), with the notable absence of ant domatia. Previously, the oldest known domatia were from the middle Eocene (ca. 49 Ma) of Victoria, Australia (O'Dowd et al. 1991). This

example is followed by late Eocene (ca. 42 Ma) acarodomatia from the same location (O'Dowd et al. 1991) and middle Eocene (ca. 44 Ma) acarodomatia from north-central Oregon, USA (Hanson 1996, Liu et al. 2014). Five younger examples of acarodomatia come from the Miocene of New Zealand (ca. 20 Ma) (Bannister et al. 2012, Conran et al. 2016, Kaulfuss 2012, Kaulfuss et al. 2015, Lee et al. 2010, Lee et al. 2012, Pole 1993, 1996), and the late Neogene to early Quaternary of Portugal (ca. 7 to 1.8 Ma) (Góis-Marques et al. 2018). The discovery of the Kaiparowits Formation acarodomatia (75.1 and 74.9 Ma, see Supplementary Material in Appendix E) is heretofore the oldest evidence of a plant–mite mutualism in the fossil record by more than 25 million years. It is also the oldest known domatia of any kind and extends the record of domatia into the Mesozoic Era.

In contrast to acarodomatia, the evolutionary history of ant domatia (myrmecodomatia) is comparatively recent. Indirect evidence indicates that myrmecodomatia evolved during the Cenozoic (Nelsen et al. 2018), perhaps in the Early Miocene (ca. 19 Ma) (Chomicki and Renner 2015). However, no myrmecodomatia are known from the fossil record. It is possible that this is a result of poor preservation potential of myrmecodomatia structures or a sampling bias toward leaves. Myrmecodomatia differ from acarodomatia in several ways. Chiefly, myrmecodomatia are not located in the vein axils of plants due, in part, to the relatively large size of ant individuals, which often are larger than a single acarodomatium. Consequently, myrmecodomatia are located in hollow stems, swollen petioles, or enlarged thorns and therefore are less restricted to certain

Figure 5.2: Illustration depicting the hypothesized host plant leaf morphology, acarodomatia and mites of the Kaiparowits Formation plant–mite mutualism. Photograph specimen EPI.45456. Scale bar, 100 µm. Illustration by M. Leggitt (Maccracken et al. 2019).

Table 5.1: Comparison of all acarodomatia reported from the fossil record.

Age	Site	Location	Host Plant Taxon	Acarodoma-tia Type	References
Late Cretaceous (75.1 Ma)	Kaiparowits Formation	Utah, USA	KP88	Pouch	This study
Middle Eocene (ca. 49—42 Ma)	Monier East Yatala Sand Pit	South Australia, Australia	Elaeocarpaceae Lauraceae	Tuft	O'Dowd et al. (1991) (O'Dowd et al. 1991)
Late Eocene (ca. 42—37 Ma)	Alcoa Coal mine	Victoria, Australia	Elaeocarpaceae Lauraceae	Tuft	O'Dowd et al. (1991) (O'Dowd et al. 1991)
Middle Eocene (ca. 44 Ma)	Clarno Formation	Oregon, USA	*Alnus clarnoensis* (Betulaceae)	**	Liu et al. (2014) (Liu et al. 2014)
Early Miocene (20 Ma)*	Manuherikia group, Foulden Maar	Otago, New Zealand	Elaeocarpaceae	**	Pole et al. (1993) (Pole 1993)
Early Miocene (20 Ma)*	Foulden Hills Diatomite, Foulden Maar	Otago, New Zealand	*Macaranga*/*Mallotus*? (Euphorbiaceae)	**	Pole et al. (1996) (Pole 1996)
Early Miocene (20 Ma)*	Foulden Hills Diatomite, Foulden Maar	Otago, New Zealand	Euphorbiaceae	Tuft	Lee et al. (2010, 2012) (Lee et al. 2010, Lee et al. 2012)
Early Miocene (20 Ma)*	Foulden Hills Diatomite, Foulden Maar	Otago, New Zealand	*Laurophyllum waipiata* (Lauraceae)	Tuft	Bannister et al. (2012) (Bannister et al. 2012)
Early Miocene (20—16 Ma)	Bannockburn Formation	Otago, New Zealand	*Malloranga dentate* (Euphorbiaceae)	Pocket	Conran et al. (2016) (Conran et al. 2016)
Mio-Pleistocene (7—1.8 Ma)	Middle Volcanic Complex; São Jorge outcrop	Madeira Island, Portugal	*Ocotea foetens* (Lauraceae)	**	Gois-Marques et al. (2018) (Góis-Marques et al. 2018)

*Foulden Maar locality age is reported in Pole et al. (1996).

**Domatia type not designated in publications.

morphological areas of the plant than acarodomatia. Myrmecodomatia also are found on a wider range of plant lineages, including monocotyledons, dicotyledons, and ferns. Nevertheless, myrmecodomatia are less common than acarodomatia, and are found on 700 plant species and 50 genera (Nelsen et al. 2018) despite the greater range of host-plant lineages. With the absence of fossil myrmecodomatia and their relatively recent evolution in the Miocene, the Kaiparowits Formation occurrences are the oldest known domatia of any kind to date.

Antiquity of plant–arthropod associations and the evolution of acarodomatia

Plant–animal mutualisms spurred, in part, the diversity of extant plants and animals (Bronstein et al. 2006, Heil et al. 2009, Ollerton 2017). Consequently, the evolution of plants coupled with plant–animal associations is a widely studied, important field within paleobiology and evolutionary biology (Kergoat et al. 2017, Labandeira 1998b, 2006b, Labandeira 2006c, Wheat et al. 2007). The most common, present-day plant–animal mutualism, pollination of seed plants by insects, originated during the Permian Period (299 to 252 Ma) (Labandeira 2010). Later, in the Mesozoic Era, the co-association of angiosperms and their insect pollinators fundamentally shaped the diversity and morphology of both groups (Bronstein et al. 2006, Ehrlich and Raven 1964). The second most common, modern plant–animal mutualism, the animal dispersal of seeds, also evolved during the Permian Period, as late Permian seeds are known from the gut cavities of tetrapods (Munk and Sues 1993, Tiffney 2004). Seed dispersal became widespread by the Mesozoic (Eriksson et al. 2000, Tiffney 2004) and increased exponentially into the Cenozoic (Tiffney 1984). In

contrast to pollination and seed dispersal, there is a substantial temporal lag between the origin of plant–mite associations and the evolution of plant–mite mutualisms.

The earliest mites (Dunlop 2010, Hirst 1923, Kethley et al. 1989, Norton et al. 1988, Schaefer et al. 2010, Walter and Proctor 1999) appear during the Early to Middle Devonian (419 to 383 Ma), when they began to interact with primitive land plants (Kevan et al. 1975, Labandeira 2007, Labandeira et al. 2014). Both predatory and fungivorous mites lineages in the Acariformes that occupy acarodomatia (Kethley et al. 1989, Norton 1985, Walter 1988) appear in the fossil record during the Paleozoic at ca. 385 Ma (Walter and Proctor 1999). Parasitiformes, which also occupy acarodomatia, first appear in the mid-Cretaceous (ca. 99 Ma) (Klompen and Grimaldi 2001, Poinar and Brown 2003). Despite hundreds of millions of years of plant–mite associations and the prevalence of predaceous and fungivorous mites since the Paleozoic, the evolution of acarodomatia apparently was delayed until the Late Cretaceous. The origin of acarodomatia likely was spurred by the evolution of angiosperms during the Late Mesozoic—albeit the probability that domatia originated before the Cretaceous is difficult to evaluate (O'Dowd and Willson 1989). The Kaiparowits Formation acarodomatia pinpoint a minimum age of 75.5 Ma (see Supplementary Material in Appendix E) for the evolution of acarodomatia.

Fossil acarodomatia are expected to occur in somewhat earlier Cretaceous floras, but the diminutive size, poor preservation of associated trichomes, and inconspicuousness associated with tufted acarodomatia might impede the detection of these structures. Given the almost exclusive occurrence of acarodomatia on living woody and arborescent dicotyledons, estimating the timing of woody and arborescent

growth forms in angiosperms arguably provides the best age constraint on the origin of acarodomatia. While the evolutionary origin of angiosperms has been dated to the Cretaceous (Magallón et al. 2015), Jurassic (Wikström et al. 2001), and even Triassic (Smith et al. 2010), the first widely accepted and abundant fossil evidence for angiosperms is palynological and dates to the mid Early Cretaceous, ca. 140 Ma (Crane et al. 1995, Herendeen et al. 2017, Hughes and McDougall 1994, Lupia et al. 1999). Herbaceous angiosperm mesofossils and macrofossils become diverse and abundant during the Barremian–Aptian transition (ca. 125 Ma) and unequivocal fossils of woody dicotyledons first appear near the Albian–Cenomanian boundary (ca. 100 Ma), although woodiness remains a rare growth habit at this time (Feild et al. 2011, Friis et al. 2011, Jud et al. 2018, Oakley and Falcon-Lang 2009, Philippe et al. 2008, Wheeler and Lehman 2009, Wheeler and Baas 1991). The first instances of woodiness around 100 Ma would suggest acarodomatia probably also evolved at this time (Barale et al. 2002, Philippe et al. 2008). This hypothesis is further supported by phylogenetically basal ANA (Amborellaceae, Nymphaeales and Austrobaileyaceae) grade angiosperms that completely lack acarodomatia, suggesting Early Cretaceous representatives of these linages also lacked acarodomatia. In contrast, some of the most basal woody lineages of magnoliid angiosperms including those in Piperales, Laurales and Magnoliales have acarodomatia (Zanella and Ferla 2013). While these clades evolved by about 125 Ma (Barale et al. 2002, Friis et al. 2011), they likely remained herbaceous until ca. 100 Ma, consistent with our hypothesis that acarodomatia evolved about 100 million year ago.

Acarodomatia arguably are a recent evolutionary innovation, much later than the pollination or seed dispersal plant–animal mutualisms, and well after the evolutionary history of other plant–mite associations (Walter 2017). Nevertheless, acarodomatia are the third-most common plant–animal mutualisms in modern ecosystems (Walter 2017). The Kaiparowits Formation acarodomatia, dated to 75.7 Ma, occur approximately 25 million years after the inferred evolution of these structures. While angiosperms are highly diverse by this time, their global rise to ecological dominance across most environments probably did not happen until the latest Cretaceous or Early Cenozoic (Johnson and Ellis 2002, Lidgard and Crane 1990, Wing et al. 1993). It is widely acknowledged that plant–animal mutualisms, specifically pollination and seed dispersal, played a seminal role in the ecological ascendency of angiosperms (Friis et al. 2011, van der Niet and Johnson 2012). Based on the function of modern acarodomatia, we suggest that plant–mite mutualisms may have contributed to the success of angiosperms in no small part by protecting these plants from elevated herbivore and fungal pressures during their evolutionary and ecological diversification.

Acknowledgments

We thank the DMNS Leaf Whackers, K. MacKenzie, N. Neu-Yagle, G. Rossetto, K. Hamby, E. Tielens, D. Gruner, S. Schachat, S. Whittaker, G. Romero, S. Zona and Y. Imada. We are also grateful to the two anonymous reviewers and the editorial board.

Chapter 6: Widespread biases in deep time plant–insect associational studies obscure potential patterns of insect preferences throughout the Age of Angiosperms

Abstract

Many recent studies have focused on discovering patterns of plant–insect interactions through deep time, but few have considered the empirical and analytical limits imposed by spatial, temporal, and sampling biases in the fossil record. Here we examine how host preferences by insect herbivores have changed throughout the Age of Angiosperms (Cretaceous Period–Quaternary Period) and with respect to floral diversity at each fossil locality. While we uncovered significant results suggesting that locality-specific insect herbivory stabilized during the last 28 million years and insect herbivory also is highly variable in diverse plant communities, these results are rendered uncertain due to inherent biases of the fossil record and differences in sampling regimes. Without consistent and accurate taxonomic information, we are not able to identify the underlying cause(s) for our significant results—they could either be real, biologically-meaningful patterns or simply artifacts of sampling. These results could (i) reflect plant communities changing through time, (ii) reflect certain clades having high or low instances of herbivory, (iii) exemplify the taxonomic bias in sampling methods that may overlook certain clades of plant hosts, or (iv) these results could reflect the difficulties of taxonomically identifying older angiosperm

plants and often implicit in the common practice of morphotyping a fossil flora. While our results do not explicitly answer our initial question of whether insect preference, as measured by richness of damage types, for host plants has occurred in deep time, it does provide avenues toward resolving this issue.

Introduction

Vascular plants and herbivorous insects are among the most biodiverse macroscopic clades of organisms and their ecological associations are a cornerstone of terrestrial ecosystems (Foottit and Adler 2009; Futuyma and Mitter 1996; Lewinsohn and Roslin 2008). The estimated global annual loss of foliage by insect herbivores is 5–18% (Coley and Barone 1996; Cyr and Pace 1993; Kozlov et al. 2015; Turcotte et al. 2014), which has profound, top-down effects on plant biomass, abundance, survival, reproduction, and diversity (Jia et al. 2018). Additionally, the diversity of ecological, biochemical, behavioral, physiological, genetic, and evolutionary underpinnings of plant–insect associations create an almost boundless prospective dataset (Strauss and Zangerl 2002) that extends to the Paleozoic Era (Labandeira 1998a; Labandeira 1998b; Labandeira 2002; Labandeira 2006; Labandeira et al. 2014). Insect herbivory has generally increased in diversity and specialization (Pinheiro et al. 2016), together with the diversification of vascular plants through time. A number of plant–insect associational studies also have documented significant changes in insect damage across particular geologic ages, regions, and relative to local plant diversities (e.g. Currano et al. 2010; Currano et al.

2008; Labandeira et al. 2002; Leckey and Smith 2017; Pinheiro et al. 2016; Wappler et al. 2009; Wappler and Grímsson 2016; Wilf and Labandeira 1999; Wilf et al. 2001). However, relatively little attention has been paid to analyzing large-scale patterns of deep time plant–insect associations, specifically insect preference for particular plant hosts through time and in relation to plant community structure.

Host plant preference by herbivorous insects, or the targeting of particular plants for herbivory, is subject to many factors, which include plant defense mechanisms (Bennett and Wallsgrove 1994; Ehrlich and Raven 1964; Kossel 1891), plant–insect coevolution (Ehrlich and Raven 1964; Farrell 1998; Janz 2011; McKenna et al. 2009; Mitter et al. 1988; Moreau et al. 2006), the degree of herbivore specialization on plant hosts (Forister et al. 2015; Jorge et al. 2017; Novotny et al. 2002a; Novotny et al. 2002b), the nutritional value of the plant (Minkenberg and Ottenheim 1990; Scheirs et al. 2003), the ability of the insect to find the plant in time and space (Feeny 1976; Miller and Strickler 1984), and the diversity of plant hosts within a particular habitat (Schallhart et al. 2012; Bach 1981). In particular, the higher the diversity of plant species in an area, as measured by the evenness and richness of plant species, the higher the productivity of that system (Huston 1997). Previous studies of deep time plant–insect associations have supported this theory to varying degrees (Currano et al. 2010; Wappler and Grímsson 2016), except in cases of extreme habitat disturbance (Wilf et al. 2006).

Insect preference is also known to have changed through time based on evidence of plant-host use across various herbivorous insect phylogenies (Bernays 1998; Eastop 1972; Eastop 1978; Wikler and Mitter 2008; Moran 1988), herbivorous

insect damage on fossil leaves (Winkler et al. 2009), and the presence of co-occurring herbivorous insect and plant lineages through time (Labandeira 2014). Notably, Labandeira (2014) compiled a list of insect families and their diet breadths across the rise and radiation of angiosperms during the Early Cretaceous Epoch and documented large-scale shifts from gymnosperm- and fern-feeders to angiosperm-feeders. Rigorous statistical methodologies to measure insect preference are now required to better quantify the role of insect preference in the fossil record through time.

A novel method, which calculates the expected richness of insect damage for ancient plant hosts is used in this study to determine insect preference for, or aversion to, fossil plant hosts throughout the Age of Angiosperms. Using a dataset compiled from 19 publications of deep time plant–insect associations, we analyze insect preference for a total of 58,882 specimens, which document a considerable time interval during the Age of Angiosperms from ca. 76 to 2 Ma. The fossil localities used in this analysis represent a range of sampling regimes and inherent difficulties with fossil plant taxonomic identifications, as well as differences in geologic ages and paleobotanical diversities. Skewedness of insect preference for plant hosts, which is measured as higher or lower than expected, is distributed unevenly through time and in relation to plant host diversities, although we ultimately question how the nature of plant–insect association datasets may influence our ability to measure broad-scale patterns of insect preferences in the fossil record.

Methods

Data Inclusion

We analyzed the datasets of 151 previously published studies on plant–insect associations from the Age of Angiosperms and five previously unpublished locality datasets generated by the lead author Maccracken (Table 6.1). The earliest, undisputed fossil angiosperm material is dated to the Early Cretaceous (ca. 136 Ma) (Crane et al. 1995; Herendeen et al. 2017; Hughes and McDougall 1994; Lupia et al. 1999), so all plant–insect associational studies from this date and younger were considered, although the earliest suitable and available datasets were ca. 76 Ma, approaching the midpoint of the occurrence of fossil angiosperms. Geographically constrained localities were selected as the unit of comparison rather than datasets from entire geologic formations, disparate time intervals, or specific regions. We considered only localities with more than 50 leaves (as in Pinheiro et al. 2016) and with at least 20 specimens of the dominant host-plant taxon. Localities with repeat excavations (ex. Loc. 1a, Loc 1b, etc.) were combined unless the excavations were separated by distances greater than 50 m or from substantially different stratigraphic positions (ex. a locality with excavations straddling an extinction event).

We surveyed over 100 published studies for potential inclusion in this study and used 19 of those datasets (Figure 6.1). We initially amassed a total of 58,882 fossil specimens from 106 localities (Table 6.1), which were selected based on four criteria: 1) a whole-flora approach was taken in each study, rather than analyzing insect damage on a single host plant species, a single instance or type of insect damage, or a small subset of specimens pulled from a larger fossil flora collection;

Table 6.1: Localities included in this study, with information on the publication, country, geologic formation, locality name, age of each locality, as well as the richness of plant hosts, specimens, and damage types.

Publication	Region/State, Country	Geologic Deposit	Locality Name	Geologic Age, Epoch	Geologic Epoch	Date Used in This Study* (Ma)	Number of Specimens	Host Plant Richness	Damage Type Richness
Adroit et al. (2016)	Hérault, France	Bernasso	Bernasso	Gelasian	Pleistocene	2	535	20	40
Adroit et al. (2018a)	Thüringen, Germany	Berga	Berga	Piacenzian	Pliocene	2.8	534	33	25
	Lower-Saxony, Germany	Willershausen	Willershausen	Piacenzian	Pliocene	2.8	7491	209	83
Wappler & Grímsson (2016)	Vesturland, Iceland	Hreðavatn-Stafholt	Brekkuá	Messinian	Miocene	6.5	184	13	12
	Vesturland, Iceland	Hre›avatn-Stafholt	Hestabrekkur	Messinian	Miocene	6.5	89	8	11
	Vestfirðir, Iceland	Skarðsströnd-Mókollsdalur	Fell	Tortonian	Miocene	8.5	58	7	4
	Vestfirðir, Iceland	Skarðsströnd-Mókollsdalur	Mókollsdalur	Tortonian	Miocene	8.5	351	17	18
	Vestfirðir, Iceland	Tröllatunga-Gautshamar	Tröllatunga	Tortonian	Miocene	10	262	9	9
	Vestfirðir, Iceland	Brjánslækur-Seljá	Brjánslækur (Barðaströnd)	Serravallian	Miocene	12	305	20	12
	Vestfirðir, Iceland	Selárdalur-Botn	Sélárdalur	Langhian	Miocene	15	174	9	10
Möller et al. (2017)	Otago, New Zealand	Hindon Maar Crater	Hindon Maar	Burdigalian	Miocene	18.8	466	27	78
	North Bohemia, Czech	Most	Břešťany	Burdigalian	Miocene	19.6	961	35	26

Knor et al. (2012)	Republic								
	North Bohemia, Czech Republic	Most	Bílina	Burdigalian	Miocene	19.6	2215	77	54
Wappler (2010)	North Rhine-Westphalia, Germany	Rott Deposit	Orsberg	Chattian–Aquitanian	Oligocene–Miocene	23	116	35	8
	North Rhine-Westphalia, Germany	Rott Deposit	Rott	Chattian–Aquitanian	Oligocene–Miocene	23	2326	101	52
Gunkel et al. (2015)	Westerwald, Germany	Enspel	Enspel	Chattian	Oligocene	24.8	1017	48	31
Domínguez (2018)	Huesca, Spain	Sariñena Formation	LV3	Chattian	Oligocene	25.4	394	13	22
	Huesca, Spain	Sariñena Formation	LV6	Chattian	Oligocene	25.4	179	26	17
	Huesca, Spain	Sariñena Formation	LVNH	Chattian	Oligocene	25.4	138	11	17
Wappler (2010)	North Rhine-Westphalia, Germany	Rott Deposit	Quegstein	Chattian	Oligocene	25.8	371	37	12
Currano et al. (2011)	Amhara Region, Ethiopia	Chilga Basin	CH72	Chattian	Oligocene	27.5	195	23	18
	Amhara Region, Ethiopia	Chilga Basin	CH90	Chattian	Oligocene	27.5	126	15	9
	Amhara Region, Ethiopia	Chilga Basin	CH92	Chattian	Oligocene	27.5	155	14	17
Currano et al. (2011)	Amhara Region, Ethiopia	Chilga Basin	CH40	Chattian	Oligocene	27.5	208	14	21
	Amhara Region, Ethiopia	Chilga Basin	CH41	Chattian	Oligocene	27.5	93	25	13

Wappler & Denk (2011)	Spitsbergen, Norway	Renardodden	Renardodden	Priabonian	Eocene	36	344	21	16
Wilf et al. (2001)	Wyoming, USA	Green River Formation	323	Lutetian	Eocene	43	179	15	11
	Wyoming, USA	Green River Formation	1732	Lutetian	Eocene	43	638	27	26
Wappler & Denk (2011)	Spitsbergen, Norway	Aspelintoppen	Nathorstfjellet	Lutetian	Eocene	44	283	14	17
	Spitsbergen, Norway	Aspelintoppen	Nordenskiöldfjellet	Lutetian	Eocene	44	277	14	18
Wappler et al. (2012)	Rhineland-Palatinate, Germany	Eckfeld Maar	Eckfeld	Lutetian	Eocene	44.3	3816	33	64
	Hesse, Germany	Messel	Messel	Yrpesian–Lutetian	Eocene	47.8	5499	93	97
Currano et al. (2019)	Wyoming, USA	Aycross	EPWR1601	Ypresian	Eocene	49.1	292	22	21
	Wyoming, USA	Aycross	EPWR1602	Ypresian	Eocene	49.1	186	17	16
	Wyoming, USA	Aycross	EPWR1603	Ypresian	Eocene	49.1	270	15	13
	Wyoming, USA	Aycross	EPWR1604	Ypresian	Eocene	49.1	160	17	17
	Wyoming, USA	Wind River	DMNH5098	Ypresian	Eocene	52.4	231	21	23
Currano et al. (2019)	Wyoming, USA	Wind River	DMNH5100	Ypresian	Eocene	52.4	373	7	29
	Wyoming, USA	Wind River	DMNH5102	Ypresian	Eocene	52.4	370	21	18
	Wyoming, USA	Wind River	DMNH5104	Ypresian	Eocene	52.4	175	19	13
Currano et al. (2010)	Wyoming, USA	Willwood	42400	Ypresian	Eocene	52.7	492	19	60
	Wyoming, USA	Willwood	42401	Ypresian	Eocene	52.7	106	10	17
	Wyoming, USA	Willwood	42402	Ypresian	Eocene	52.7	100	6	16
	Wyoming,	Willwood	42403	Ypresian	Eocene	52.7	476	19	57

	USA								
	Wyoming, USA	Willwood	42404	Ypresian	Eocene	52.7	102	8	16
	Wyoming, USA	Willwood	42405	Ypresian	Eocene	52.7	495	15	54
Wilf et al. (2001)	Utah, USA	Wasatch Formation	41342	Ypresian	Eocene	53	343	13	15
	Utah, USA	Wasatch Formation	41352	Ypresian	Eocene	53	438	16	20
Currano et al. (2010)	Wyoming, USA	Willwood	37560	Ypresian	Eocene	53.4	693	15	56
	Wyoming, USA	Willwood	37654	Ypresian	Eocene	54.2	250	13	17
Schmidt et al. (2019)	Wyoming, USA	Hanna	E	Ypresian	Eocene	54.5	323	17	18
Currano et al. (2008)	Wyoming, USA	Willwood	42384	Ypresian	Eocene	55.8	995	28	38
	Wyoming, USA	Fort Union	41643	Ypresian	Eocene	55.9	767	15	12
Wilf et al. (2001)	Wyoming, USA	Fort Union	41270	Thanetian–Ypresian	Paleocene–Eocene	56	345	9	23
Currano et al. (2010)	Wyoming, USA	Willwood	42411	Thanetian	Paleocene	56.4	1015	19	30
Currano et al. (2008)	Wyoming, USA	Fort Union	42042	Thanetian	Paleocene	57.5	1298	14	26
Schmidt et al. (2019)	Wyoming, USA	Hanna	C	Thanetian	Paleocene	58.0	304	13	21
Currano et al. (2008)	Wyoming, USA	Fort Union	42041	Thanetian	Paleocene	58.9	907	7	19
Schmidt et al. (2019)	Wyoming, USA	Hanna	A	Selandian	Paleocene	59.5	92	13	9
Wappler et al. (2009)	Menat, France	Menat Lagerstatte	Menat Pit	Selandian	Paleocene	60.5	791	74	37
Wappler & Denk (2011)	Spitsbergen, Norway	Firkanten	Kolfjellet	Selandian	Paleocene	61.0	335	17	19
Donovan et	Patagonian Argentina	Peñas Coloradas	LF	Danian	Paleocene	62.4	568	29	42
	Patagonian	Salamanca	PL1	Danian	Paleocene	64.1	1089	29	48

al. (2018)	Argentina								
	Patagonian Argentina	Salamanca	PL2	Danian	Paleocene	65.2	1137	31	54
Labandeira et al. (2002a)	North Dakota, USA	Fort Union	441	Danian	Paleocene	65.6	90	10	9
	North Dakota, USA	Fort Union	562	Danian	Paleocene	65.6	78	7	13
	North Dakota, USA	Fort Union	898	Danian	Paleocene	65.6	173	9	12
	North Dakota, USA	Fort Union	2217	Danian	Paleocene	65.6	296	23	13
	North Dakota, USA	Fort Union	86107	Danian	Paleocene	65.6	457	17	14
	North Dakota, USA	Fort Union	86110	Danian	Paleocene	65.6	297	12	17
	North Dakota, USA	Fort Union	87150	Danian	Paleocene	65.6	544	11	8
	North Dakota, USA	Fort Union	88103	Danian	Paleocene	65.6	86	11	6
	North Dakota, USA	Fort Union	KJ8403	Danian	Paleocene	65.6	67	8	8
	North Dakota, USA	Fort Union	2212	Maastrichtian	Late Cretaceous	66.5	67	12	9
	North Dakota, USA	Fort Union	86100	Maastrichtian	Late Cretaceous	66.5	508	21	17
	North Dakota, USA	Fort Union	86102	Maastrichtian	Late Cretaceous	66.5	190	18	11
	North Dakota, USA	Fort Union	86153	Maastrichtian	Late Cretaceous	66.5	155	13	13
	North Dakota, USA	Fort Union	87110	Maastrichtian	Late Cretaceous	66.5	62	8	10
	North Dakota, USA	Fort Union	87129	Maastrichtian	Late Cretaceous	66.5	104	15	8
	North Dakota, USA	Fort Union	87134	Maastrichtian	Late Cretaceous	66.5	172	14	17
Labandeira et al. (2002a)	North Dakota, USA	Fort Union	88111	Maastrichtian	Late Cretaceous	66.5	70	11	3
	North Dakota, USA	Hell Creek	1489	Maastrichtian	Late Cretaceous	66.5	102	26	16

Labandeira et al. (2002a)	North Dakota, USA	Hell Creek	1491	Maastrichtian	Late Cretaceous	66.5	269	17	23
	North Dakota, USA	Hell Creek	1781	Maastrichtian	Late Cretaceous	66.5	117	18	14
	North Dakota, USA	Hell Creek	1855	Maastrichtian	Late Cretaceous	66.5	123	10	21
	North Dakota, USA	Hell Creek	2087	Maastrichtian	Late Cretaceous	66.5	349	33	14
	North Dakota, USA	Hell Creek	2097	Maastrichtian	Late Cretaceous	66.5	245	15	18
	North Dakota, USA	Hell Creek	2098	Maastrichtian	Late Cretaceous	66.5	123	17	15
	North Dakota, USA	Hell Creek	2099	Maastrichtian	Late Cretaceous	66.5	76	15	8
	North Dakota, USA	Hell Creek	2203	Maastrichtian	Late Cretaceous	66.5	392	17	18
	North Dakota, USA	Hell Creek	428	Maastrichtian	Late Cretaceous	66.5	708	67	32
	North Dakota, USA	Hell Creek	517	Maastrichtian	Late Cretaceous	66.5	134	16	9
	North Dakota, USA	Hell Creek	566	Maastrichtian	Late Cretaceous	66.5	114	20	8
	North Dakota, USA	Hell Creek	567	Maastrichtian	Late Cretaceous	66.5	373	24	21
	North Dakota, USA	Hell Creek	568	Maastrichtian	Late Cretaceous	66.5	139	21	22
	North Dakota, USA	Hell Creek	571	Maastrichtian	Late Cretaceous	66.5	279	21	24
	North Dakota, USA	Hell Creek	897	Maastrichtian	Late Cretaceous	66.5	123	16	18
	North Dakota, USA	Hell Creek	900	Maastrichtian	Late Cretaceous	66.5	470	44	31
Donovan et al. (2018)	Patagonian Argentina	Lefipán	LefE	Maastrichtian	Late Cretaceous	66.5	606	41	45
	Patagonian Argentina	Lefipán	LefL	Maastrichtian	Late Cretaceous	66.5	108	26	28
	Patagonian Argentina	Lefipán	LefW	Maastrichtian	Late Cretaceous	66.5	140	30	28
	New Mexico,	Fruitland/	302	Campanian	Late	74.3	66	15	7

This study	USA	Kirtland			Cretaceous				
	New Mexico, USA	Fruitland/ Kirtland	9726	Campanian	Late Cretaceous	74.3	189	42	20
	Utah, USA	Kaiparowits	Lost Valley	Campanian	Late Cretaceous	75.6	3918	79	78
	Utah, USA	Kaiparowits	Caveat Friendship	Campanian	Late Cretaceous	75.6	502	55	34
	Utah, USA	Kaiparowits	JARS	Campanian	Late Cretaceous	75.7	719	70	51

*Dates for each locality were obtained from the original publications. When a geologic interval or range of dates was given, we calculated the mean, using the Geological Society of America's Geological Time Scale v. 5.0 when necessary (Walker et al. 2018).

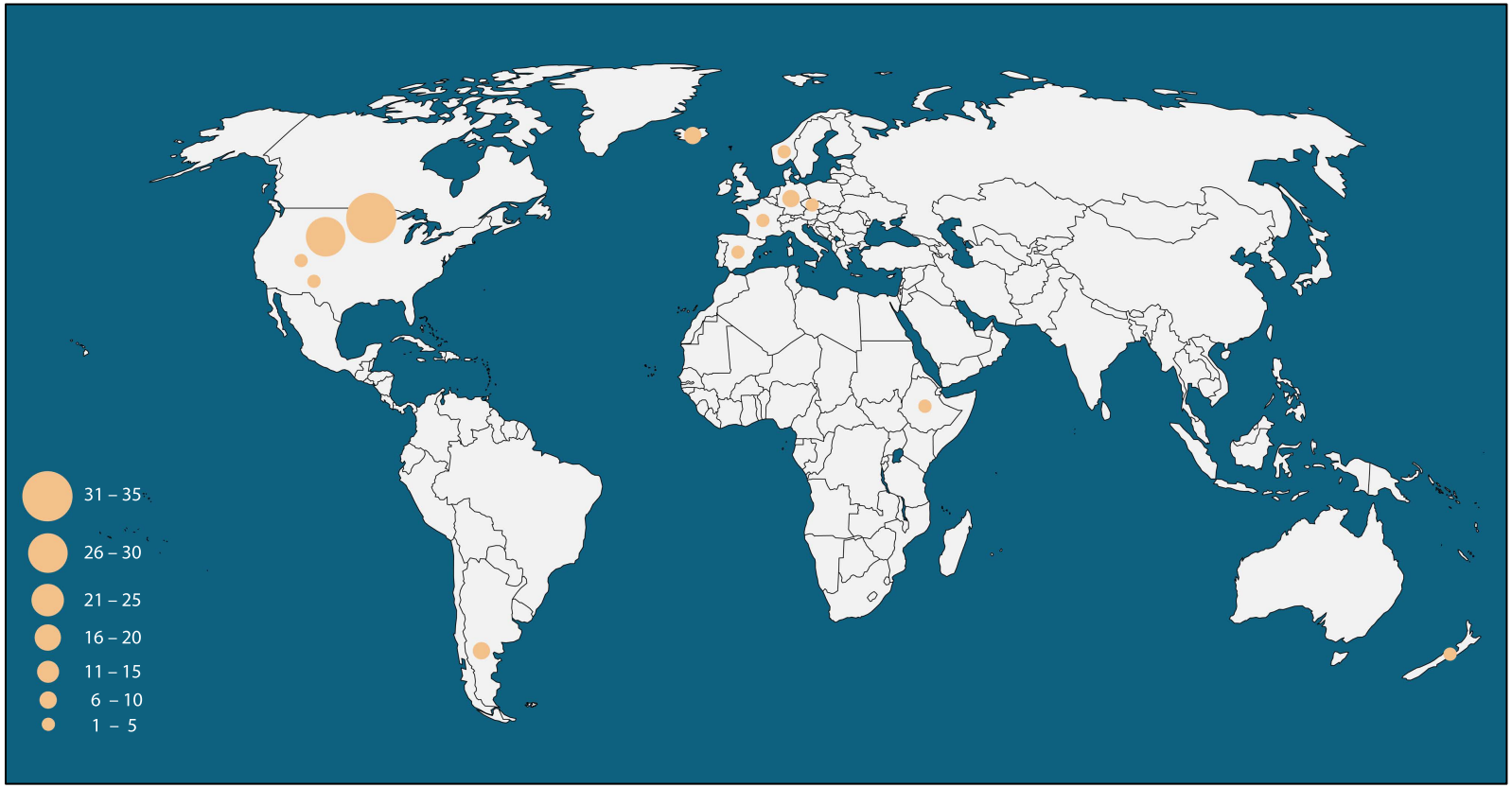


Figure 6.1: Map of localities analyzed in this study. Circles represent approximate number of localities per region.

2) the study used the damage type schema from the *Guide to Insect (and Other) Damage Types on Compressed Plant Fossils* (Labandeira et al. 2007); 3) the sites were from either the Mesozoic or Cenozoic Eras, in which angiosperms were typically a dominant component of the floras; and 4) data were publicly available or authors shared their data via personal correspondence. We attempted to incorporate all relevant studies in the analysis, but some studies may have been unintentionally overlooked. Additionally, not all authors responded to our request for data, consented to share data from previously published studies, or provided datasets that were setup in such a way that they could not be incorporated into this study.

We obtained the geologic age for each locality from the original publications. In cases where a range of dates was given, we calculated the mean from the geological time interval provided. Furthermore, when only a geologic stage was provided, we used the midpoint date of the stage range. Occasionally, dates were estimated from locality placement on stratigraphic columns or external stratigraphic publications. Geologic dating across these localities varied in accuracy, attributable to poor stratigraphic context of the floras, obsolete dating methods or studies, and excessively large error estimates. The variability of the geologic dating was inherent in a study of this scale and we assumed that this variability did not alter the results in a meaningful way.

We used the assigned plant-host taxonomic identifications from the publications, but attempted to correct all misspelled specimen data within reason and based on the species already present in a particular dataset (ex. "*Alus* sp." to "*Alnus* sp."). Indeterminate leaves that could not be morphotyped (ex. "indeterminate sp.")

were excluded from the analyses and subspecies identifications were lumped back into their respective species. Data were otherwise unaltered and we did not check damage type analyses for accuracy. Statistics reported in the publications occasionally differed from the datasets, such as differences in number of specimens or number of plant-host species. In these cases we used the datasets because it was impossible to identify the inconsistencies.

Taxonomy (family, order) of each plant host was compiled using the package "taxize" for *R* statistical software (Chamberlain et al. 2017; R Development Core Team 2013). Plant hosts that could not be identified by "taxize" were added by hand, which frequently happened for extinct genera. We obtained taxonomic information for extinct taxa from the peer-reviewed publications, Fossilworks (Alroy 2016), or academic institution websites. We also compiled the clade of each plant host (fern, gymnosperm, magnoliid angiosperm, monocotyledonous angiosperm, or eudicotyledonous angiosperm). However, the category of "dicotyledonous angiosperm" was not used as it creates a paraphyly stemming from the exclusion of the monocots (Soltis and Soltis 2004). Additionally, we did not compile taxonomic information for a number of morphotyped plant hosts, such as "monocot sp.", "conifer 1", etc., although the relevant clade was sometimes evident based on the morphotype labels.

We noted the presence of nitrogen-fixing plant species, which are known to influence the level of insect herbivory due to higher leaf Nitrogen : Carbon ratios (Currano et al. 2016), in the dataset. Legumes (Fabaceae) are well known for their symbiotic mutualism with soil-dwelling rhizobia to fix atmospheric nitrogen (Duggar

and Davis 1916; Russell 1894). However, not all legumes possess the ability to fix nitrogen, with early diverging lineages having low percentages of nitrogen fixing species compared to more recently diverging lineages (Bryan et al. 1996). A recent reclassification of Fabaceae sinks the mimosoid clade within the subfamily Caesalpiniodeae (LPWG 2017), meaning that the Caesalp clade has a greater number of nitrogen fixing species. Formerly, the Mimosoid clade had ~90% nitrogen fixing species (~2700 species), while the Caesalp clade had ~23% nitrogen fixing species (~460 species). In this study, we categorized the legume taxa identified to the Caesalp clade as being non-nitrogen fixing because many of the identifications were made before the Mimosoid clade was sunk into the Caesalp clade, and therefore the likelihood of those taxa being non-nitrogen fixing members of the clade was high. Some non-legume plant clades also have evolved the ability to form symbiotic relationships with microbes to fix nitrogen: including cycads, *Gunnera* (Gunneraceae) (Bergman et al. 1996; Bergman et al. 2007; Santi et al. 2013), *Azolla* (Salviniaceae), *Alnus* (Betulaceae), *Rubus* (Roseaceae), and approximately twenty other less common genera (Bond 1983; Sprent and Parsons 2000).

Data Analyses

To assess if there was a general relationship between insect herbivory and time, we regressed an index of damage-type diversity against the geologic age of all localities. Within each of the 164 localities, we then ranked plant hosts by abundance from the most abundant to least abundant plant host. A cutoff of a 20 specimen minimum for the most abundant plant host was implemented and 106 localities met this cutoff (Table 6.1). This helped to eliminate heavily cherry-picked fossil floras

that underrepresented the most common taxon. Next, skewed levels of herbivory, or those that fell outside of an expected range, were calculated for each plant host at each locality. For each locality, we produced a vector comprising each plant host specimen, either a taxonomically identified species or morphotype, and an adjacent matrix of the presence or absence of damage types for that specimen. To generate the p-value, we then randomly shuffled the vector (plant host specimens) 50,000 times to determine what proportion of the time we found more herbivory or less herbivory per plant host, as measured by the richness of damage types in the matrix, than that of the original data. This allowed us to only compare levels of herbivory for a plant host in relation to the other plant hosts for their particular locality, since heterogeneity of ecological and evolutionary factors among the localities would render whole-dataset comparisons meaningless. Taxa represented by 5 or fewer specimens were removed from the dataset due to insufficient sample sizes for plant-host analyses. To calculate the expected proportion of type I errors, a False Discovery Rate was used on the data (García 2004; Verhoeven et al. 2005) and significance was reached at $p \leq 0.0111$.

After plant hosts with significantly skewed levels of herbivory were found, localities were categorized as either having at least one plant host with skewed levels of herbivory or having no plant hosts with skewed levels of herbivory. Two empirical cumulative distributions were then calculated: one for the localities that have plant hosts with significantly skewed levels of herbivory and one for the localities without plant hosts that have significantly skewed levels of herbivory. To test for differences between the two distributions, and because we are comparing distributions with

continuous measures, a Wilcox rank sum test with continuity correction was calculated for the ages of these two distributions.

Three diversity indices were calculated for the diversity of plant hosts at each fossil locality (Table 6.2). These were chosen because they are commonly used in neontological ecology studies. Once the diversity of each locality was calculated, a Wilcox rank sum test with continuity correction was calculated for the diversity index and the distribution of localities that included plant hosts with significantly skewed levels of insect herbivory. Finally, a linear regression was calculated for the geologic ages and diversity indices for subsampled localities to determine if these variables were strongly correlated with one another. All plots were was produced with the R package "ggplot2" (R Development Core Team 2013).

Table 6.2: Diversity metrics calculated in this study.

Diversity Metric	Equation	Variables
Simpson's Index (*D*)	$1/\sum_{i=1}^{s} p_i^2$	*s* is the number of plant hosts at a locality, p_i is the proportion of individuals of the *i*th plant host
Shannon's Index (*H'*)	$-\sum_{i=1}^{s} p_i \ln p_i$	*s* is the number of plant hosts at a locality, p_i is the proportion of individuals of the *i*th plant host
Hill numbers (^qD *or* ^qH)	$\left(\sum_{i=1}^{s} p_i^q\right)^{1/(1-q)}$	*s* is the number of plant hosts at a locality, p_i is the proportion of individuals of the *i*th plant host, and *q* is the 'order' of the diversity metric

Results

There was no correlation (R^2=0.004, p=0.51) between the overall damage-type diversity and geologic age of all subsampled localities, which span from ca. 76–2 Ma. We next conducted analyses within each locality to better understand general patterns of plant–insect associations in deep time.

There was a total of 291 plant hosts, from 79 localities, which had significantly skewed (higher or lower) levels of herbivory based on random chance (Figure 6.2; Supplementary Tables 6.1, 6.2). The majority of these significant results were for plant hosts with lower than expected herbivory (255 plant hosts), while only 36 plant hosts exhibited higher than expected levels of herbivory. Overall, the majority of plant hosts with significantly lower levels of herbivory than expected were the more abundant taxa at the localities, whereas those with significantly higher levels of herbivory were often the relatively rarer taxa (Supplementary Figure 6.1).

Several plant lineages were disproportionately likely to have skewed herbivory that was lower than expected (Supplementary Table 6.2), including those in the gymnosperm order Pinales, the extinct Lauraceae genus *Daphnogene*, the extinct Magnoliidae morphogenus *Laurophyllum*, several monocot plant hosts, and a seemingly random assortment of eudicotyledons. Only 23% of the total plant hosts with low levels of herbivory for which we had taxonomic information belonged to the taxa listed above. Alternatively, plant hosts belonging to the asterid order Cornales were significantly more likely to be the target of herbivory (Supplementary Table 6.1); over 10% of Cornales specimens had elevated levels of herbivory, yet only 27%

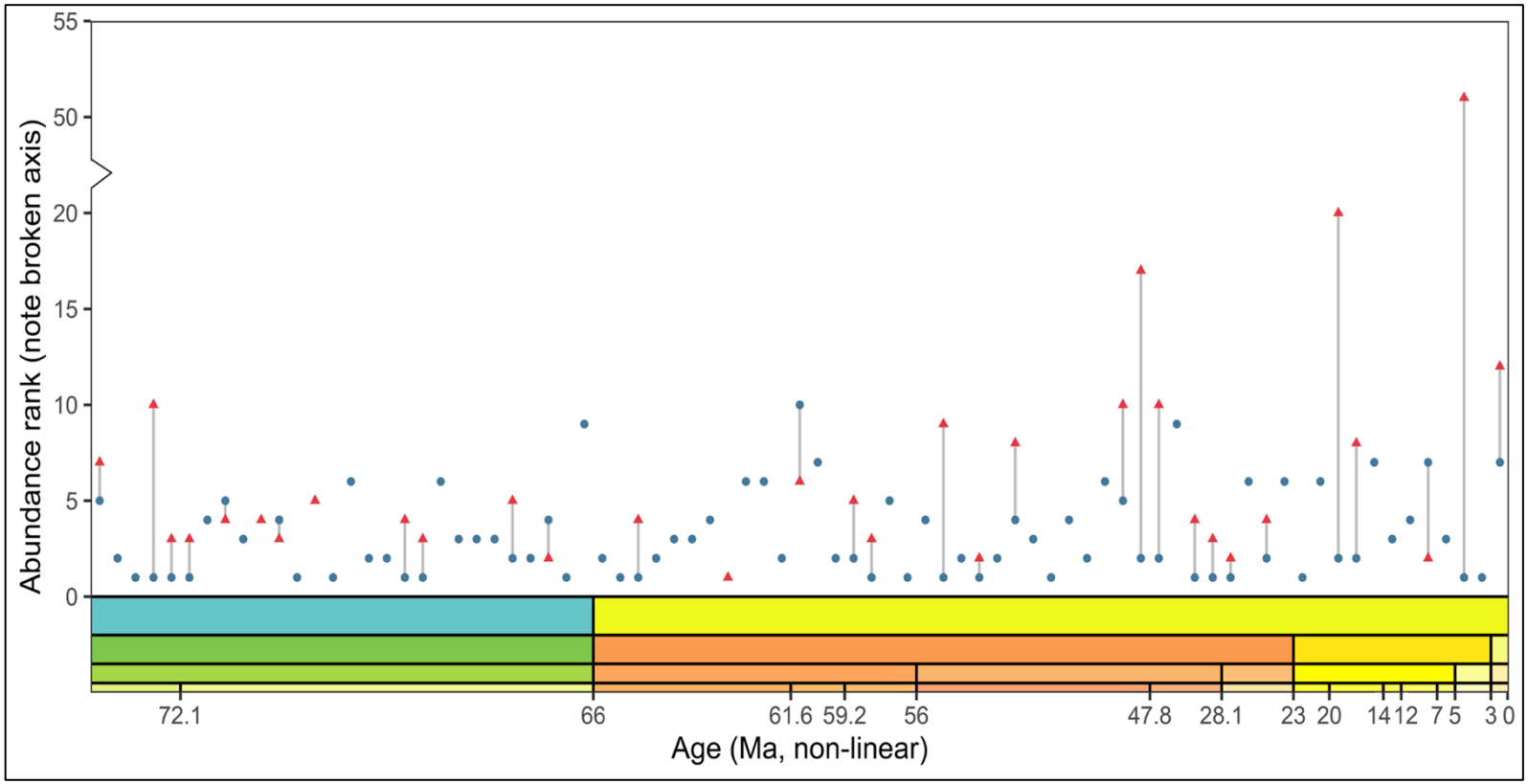


Figure 6.2: Abundance rank of plant hosts that have significantly less (blue dot) and/or significantly more (red triangle) through time (Ma). Note non-linear x- and y-axes.

of highly herbivorized plants for which we have taxonomic information belong to Cornales. Interestingly, nitrogen-fixing species were not found to have significantly higher or lower than expected levels of insect herbivory. The majority of plant hosts with skewed levels of herbivory were not taxonomically identified; of all 79 sites for which we obtained significant results for at least one taxon, 56 lacked plant-host taxonomic information and only 23 included taxonomic information.

There was a significant difference of the distributions through time between the localities that include plant hosts with skewed levels of herbivory and the distribution of localities that do not have plant hosts with skewed levels of herbivory (Wilcox Rank Sum Test with continuity correction, p=0.02) (Figure 6.3). The older localities, those between ca. 76–28 Ma, had a greater proportion of localities that include plant hosts with skewed levels of herbivory, whereas the younger localities had many fewer of these localities. For the localities over 50 Ma for which we get significant results for at least one taxon, 46 localities lack plant host taxonomic information and a scant 12 include taxonomic information.

Localities with greater plant host diversity, as calculated by the Simpson's Index (*D*), were also significantly more likely to contain plant hosts with significantly skewed levels of herbivory (p = 0.01955) (Figure 6.4). This result was also found when employing Shannon's Index (*H'*) (p = 0.009044). Both *D* and *H'* can be converted to an "effective number of species": the number of species that would produce the empirical value of the diversity index if all species were equally abundant (Hill, 1973). Many ecologists prefer the effective number of species over diversity

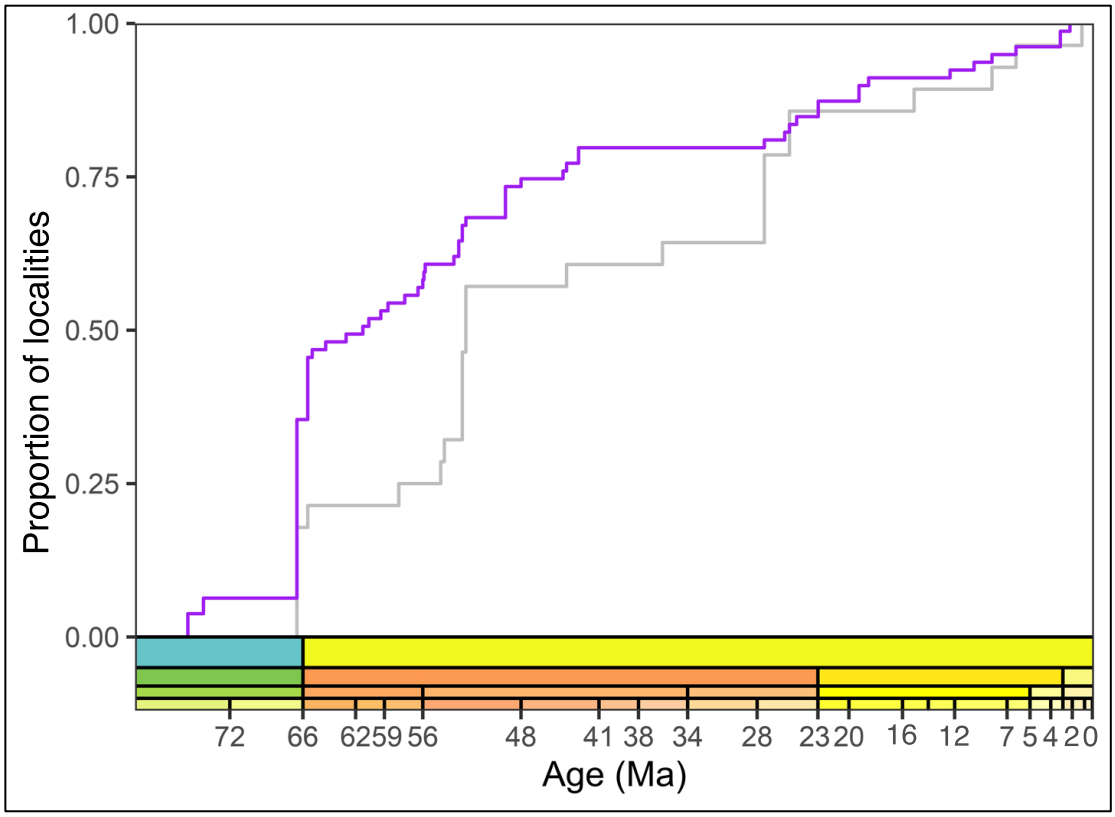


Figure 6.3: Distributions of localities through time (Ma) for localities with significantly skewed plant hosts (purple line) and localities without significantly skewed plant hosts (gray line). Note non-linear y-axis.

indices because the effective number of species has a linear relationship with total species diversity (Jost, 2006). When *D* and *H'* are converted to effective numbers of species, the p-values that relate diversity to the presence of plant hosts with significantly skewed levels of herbivory remain unchanged. This is because the Wilcox rank sum test generates p-values from the rank of each locality rather than its raw *D, H'*, or effective number of species, and the rank of each locality does not change when a diversity index is converted to an effective number of species. However, geologic age and plant diversity per locality were not strongly correlated (R^2=0.005288; p = 0.45883) (Figure 6.5), meaning that these variables are largely independent of one another.

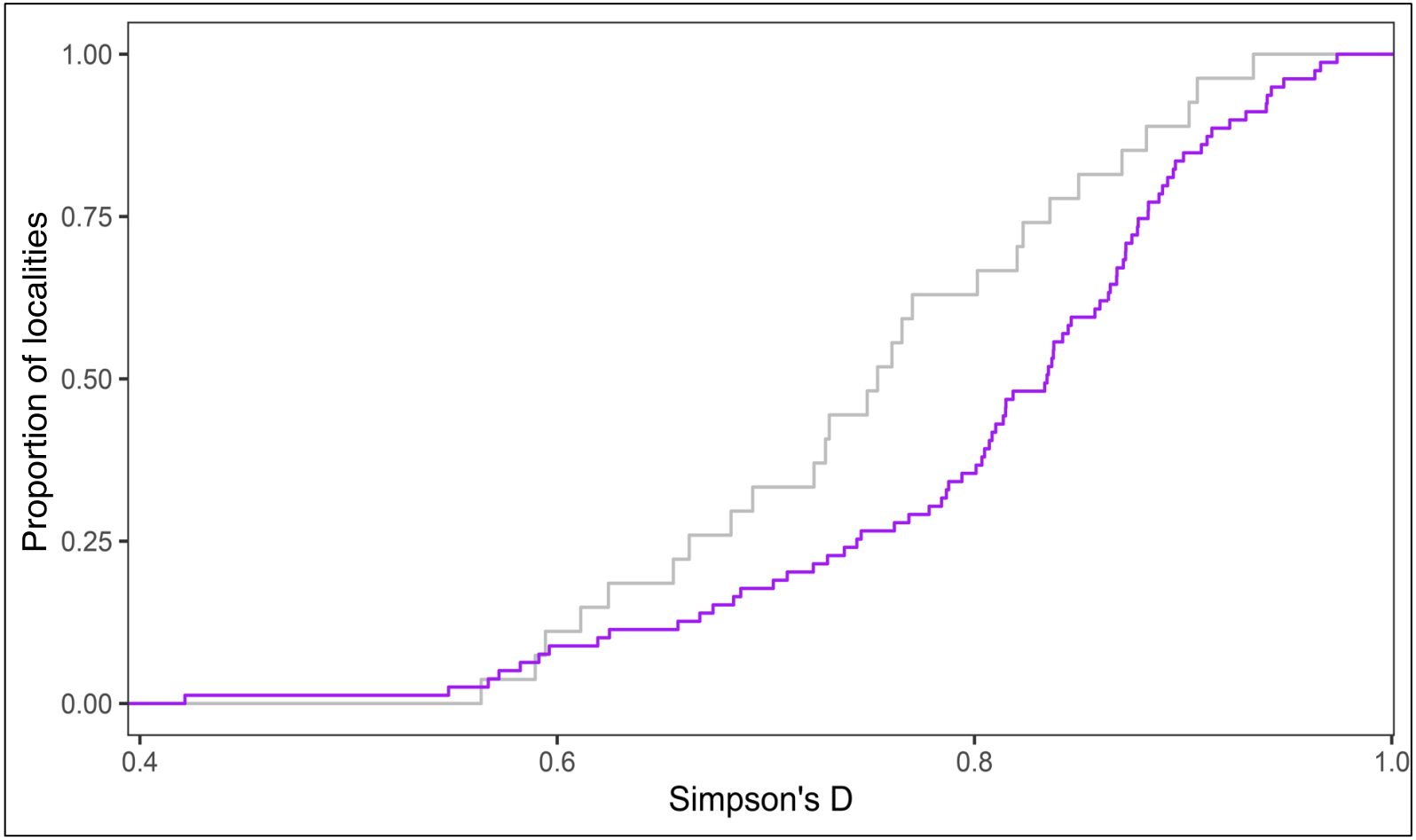


Figure 6.4: Distributions of localities by plant community diversity (Simpson's D) for localities with significantly skewed plant hosts (purple line) and localities without significantly skewed plant hosts (gray line).

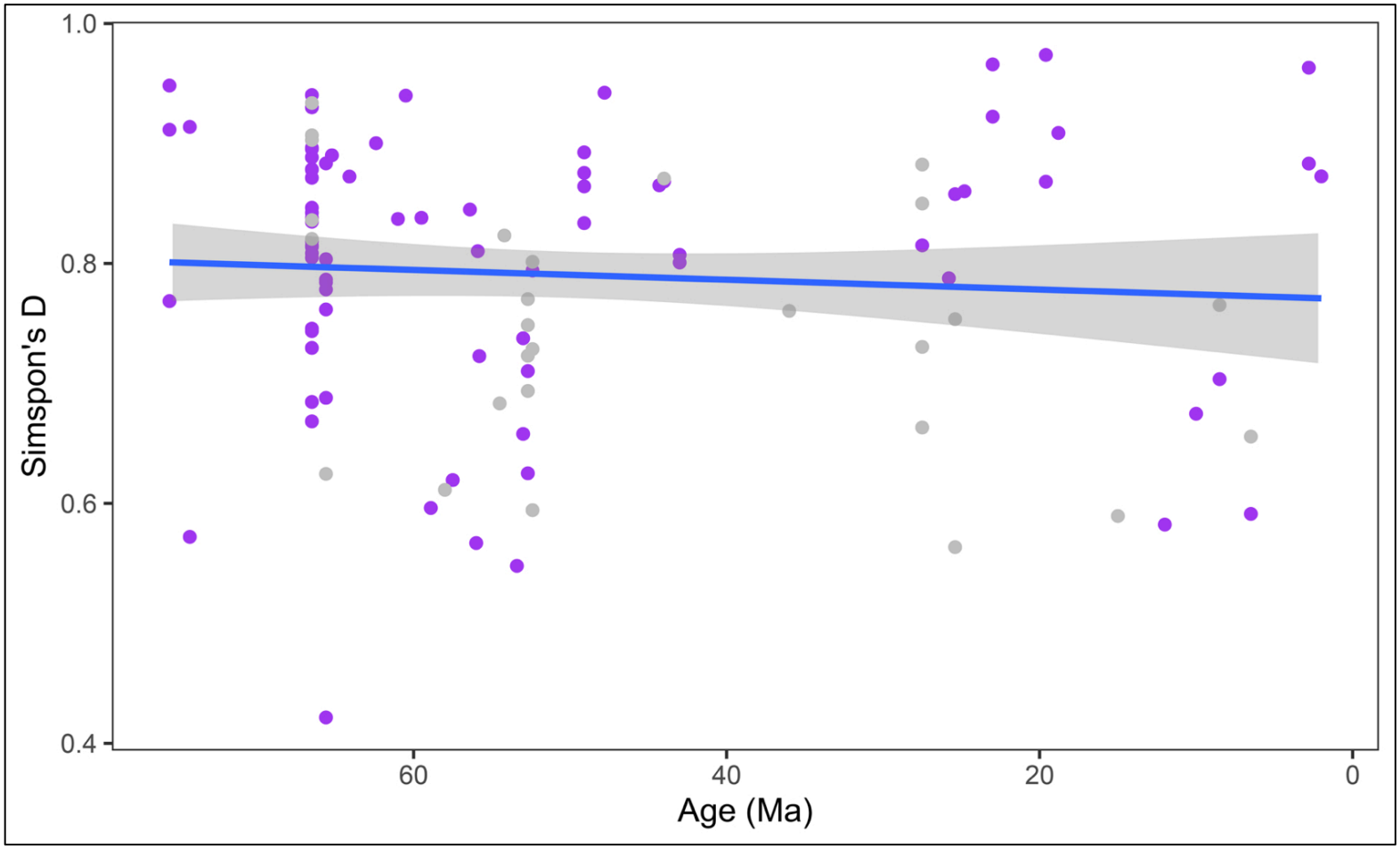


Figure 6.5: Regression of plant community diversity (Simpson's D) for each locality through time (Ma) with 95% confidence intervals (R^2=0.005288; p = 0.45883). Localities with significantly skewed plant hosts are represented by purple dots and localities without significantly skewed plant hosts are represented by gray dots.

Discussion

A broadly-held assumption in the field of plant–insect associations is that there has been widespread changes from the Cretaceous to the present-day in the diversities of angiosperms, their insect herbivores, insect damage, and insect plant-host preference, changes attributable to a coevolutionary arms race (Ehrlich and Raven 1964; Farrell 1998; Janz 2011; McKenna et al. 2009; Mitter et al. 1988; Moreau et al. 2006). We did not find a meaningful correlation between geologic age and the diversity of insect herbivory. Instead, we found that levels of insect herbivory were increasingly skewed for plant hosts at localities with older geologic ages and also for localities with higher plant-host diversities. However, these results are not necessarily clear-cut and this is a cautionary anecdote for the analyses of deep time plant–insect associations.

Fossil Record Quality and Sampling Biases as a Function of Age

Paleobotanical datasets invariably introduce difficult to control, and often problematic, variables (DiMichele and Gastaldo 2008), including paleolatitude, temperature, precipitation levels, ecosystem type, seasonality, atmospheric carbon dioxide, depositional environment, areal extent of the fossil deposit, time averaging, taphonomic setting, preservational quality of the plant specimens, and evolutionary histories (ex. Behrensmeyer et al. 2000; Locatelli 2014). These conditions almost certainly differ among each of the localities and make comparisons increasingly problematic, but may be analyzed in further studies as predictor models. Moreover, the probability of an organism becoming preserved as a fossil is "vanishingly small" (Raup 1979), although the fossil record tends to increase in completeness, quality,

and our ability to identify specimens taxonomically towards the Recent (Kidwell and Holland 2002; Raup 1979; Raup 1972). This phenomenon, known as the Pull of the Recent, explains the factors that lead to an often-artificial increase in diversity of organisms through time approaching the Recent (Raup 1979), which are pertinent to the paleobotanical datasets analyzed in this study. Factors contributing to the Pull of the Recent include the more fully developed taxonomy of extant taxa (Raup 1979). Plant hosts in younger floras often closely resemble and may indeed be closely related to extant taxa and are more easily identified and characterized by paleobotanists (Niklas and Tiffney 1994), especially in the case of angiosperm plant hosts. For example, the datasets analyzed in this study substantially increase in the proportion of identified taxa from older to younger studies.

Human error and sampling biases are also of great concern. Beyond inherent differences in data collection among researchers (judgment calls, access to various equipment, etc.) there are substantial differences in how plant-host specimens are analyzed. Museum paleobotanical collections are often fraught with sampling biases, as researchers typically over-collect the rare plant taxa and underrepresent common plant taxa, commonly referred to as 'cherry picking' (Labandeira et al. 2002). Within paleobotanical collections and sampling regimes, there also may also be preference to analyze particular clades of host plants. For instance, some researchers prioritize eudicotyledonous and magnoliid angiosperms, but exclude monocotyledonous angiosperms and non-angiosperms, in order to keep analyses as consistent with other such studies and constrained as possible (ex. Adroit et al. 2016; Wappler and Grímsson 2016; Wilf et al. 2006). Although this sampling regime is practical, it does

make comparisons with studies that include all plant host clades tenuous, and more troublingly, not all publications have explicitly disclosed this sampling bias. Finally, morphotyping, which is often implemented for older floras, limits our ability to compare such localities to those with extensive taxonomic identifications. Although species richness of morphotyped floras can be assessed, more fine scale analyses involving specific clades of plants are often not feasible.

Our results show a greater proportion of localities with skewed levels of herbivory from ca. 75–28 Ma, and that the younger localities from ca. 28–2 Ma have more stable levels of herbivory. The fundamental question we ask is: why do we see this change in insect preference through time? Because of issues with sampling, such as that the majority of plant hosts with skewed levels of herbivory were not taxonomically identified especially for sites over 50 Ma and the proportion of disproportionate herbivory for identified plant hosts also was relatively low (23% for disproportionately unherbivorized taxa and 27% for disproportionately herbivorized taxa), it is impossible to differentiate between potential explanations for our results. These explanations may be: 1) older localities include more of the plant hosts with skewed levels of insect herbivory, i.e. those belonging to Pinales, *Daphnogene*, *Laurophyllum*, and/or monocotyledons; 2) older localities were more likely to have the particular eudicotyledon plant hosts with skewed levels of herbivory due purely to random chance; or 3) researchers involving younger localities were more likely to exclude non-eudicotyledonous plant hosts, eliminating a large portion of the plant hosts that often had significant results. We cannot affirm that the increased variability of insect herbivory at older localities was the result of insect preferences for or

against particular plant taxa, as it may be the result of sampling biases and/or increasing taxonomic uncertainties with geologic age.

Plant Community Diversity and Insect Herbivory

The relationship between ecological productivity and species richness is studied widely in modern ecosystems (ex. Cardinale et al. 2011; Waide et al. 1999). Arguments for why, in general, as species richness increases the productivity also increases focus on resource complementarity and the "selection probability effect" (Huston 1997). Resource complementarity is the differentiated resource use between species in higher diversity systems leading to greater productivity per species than if that system were less diverse, whereas "selection probability effect", or sampling effect, is the increased probability of an exceptionally productive species occurring in a diverse system (Huston 1997). Waide et al. (1999) only found empirical evidence for the "selection probability effect", although resource complementarity is still widely discussed in ecological literature (ex. Ashton et al. 2010; Barry et al. 2019; Peralta et al. 2014; Poisot et al. 2013).

We asked if there was also a positive relationship between plant host richness and insect herbivory in deep time and found that increasingly diverse localities were more likely to contain plant hosts with disproportionate levels of herbivory. There was a significant difference between the distributions of localities with and without plant hosts having disproportionate levels of herbivory and plant host diversity (Simpson's *D*). These results might at first glance support the idea that as plant host diversity increases, the probability of including a plant species with skewed levels of herbivory also increases. However, these results are unsubstantiated; localities with

significant results were over two times as likely to omit taxonomic identifications of plant hosts, and the majority of the significant results occurred in localities over 50 Ma, which were four times as likely to omit taxonomic identifications of plant hosts. Despite plant-host diversity at these localities staying relatively constant through time, the distribution and lack of taxonomic resolution of plant hosts through time again poses an insurmountable problem. We cannot differentiate between several explanations, which are similar to those posed above: 1) localities with higher plant diversity were more likely to contain the plant hosts with skewed levels of insect herbivory, i.e. those belonging to Pinales, *Daphnogene*, *Laurophyllum*, and/or monocotyledons; 2) localities with higher plant diversity were more likely to have the particular eudicotyledon plant hosts with skewed levels of herbivory due purely to random chance; or 3) researchers that excluded non-eudicotyledonous plant hosts both eliminated many of the plant hosts that were found to have skewed levels of herbivory and also artificially skewed the plant-host diversities at each locality, potentially rendering this comparison meaningless.

Patterns of Insect Herbivory at Finer Temporal and Spatial Scales

Multiple studies have found significant relationships between plant–insect associations and floral diversity or geologic age, and in conjunction with other abiotic and biotic factors that are linked with geologic age (ex. Currano et al. 2010; Currano et al. 2008; Labandeira et al. 2002; Leckey and Smith 2017; Pinheiro et al. 2016; Wappler et al. 2009; Wappler and Grímsson 2016; Wilf and Labandeira 1999; Wilf et al. 2001). This study, which drew from datasets collected across many regions and time intervals, could not detect significant relationships that have been detected at

finer temporal and spatial scales, or for those which used different methodologies. For example, Pinheiro et al. (2016) found that herbivory frequency increased through time from the Devonian until the Paleocene–Eocene boundary, then decreased during the Eocene (Pinheiro et al. 2016). That study postulated that herbivory was associated with changes in global temperature, atmospheric CO_2, and O_2 availability (Pinheiro et al. 2016), not simply an increase of herbivory from the Paleozoic to the Cenozoic. Indeed, many studies have looked at plant–interactions through time, but as a function of insect herbivory in response to abiotic and biotic factors instead of insect herbivore preference through time (ex. Currano et al. 2010; Currano et al. 2008; Labandeira et al. 2002; Leckey and Smith 2017; Wappler et al. 2009; Wappler and Grímsson 2016; Wilf and Labandeira 1999; Wilf et al. 2001).

Previous studies that explicitly tested the relationships between insect herbivory and plant community diversity have produced varying results. Wappler and Grímsson (2016) found that in Icelandic Neogene deposits, plant diversity and the number of damage types were positively related ($r=0.76$; $p= 0.0001$), and that the plant diversity changed through time in response to long-term global cooling in the Neogene. In particular, they found that the structural complexity of diverse herbaceous localities increased insect herbivory, even when the patterns of global cooling led the authors to predict otherwise (Wappler and Grímsson 2016). Another study, Currano et al. (2010), measured insect damage richness against floral diversity for the Paleocene-Eocene Thermal Maximum (PETM) in the Bighorn Basin of Wyoming, USA. They found that insect herbivory was influenced by mean annual temperature (MAT) ($R^2=0.89$; $p<0.01$) more so than floral diversity ($R^2=0.38$;

p=0.08) (Currano et al. 2010). A later study by Currano et al. (2019) found that the low-diversity Big Horn Basin flora had a higher diversity of damage types compared to the two, more diverse Wind River Floras (Currano et al. 2019). Currano et al. (2019) hypothesized that this was most likely attributable to microhabitat differences between the sites or endemism of populations that were bisected by high altitude mountain passes (Currano et al. 2019). Perhaps the most striking example of insect herbivory and plant diversity occurs in early Paleocene localities 1 to 2 Ma after the Cretaceous/Paleogene extinction event (Wilf et al. 2006). Wilf et al. (2006) found unbalanced food webs at the Castle Rock and Mexican Hat Floras; there was a positive relationship between insect damage and plant diversity for the Cretaceous through Paleocene floras, except the Castle Rock Flora was exceptionally diverse and had extremely low levels of insect herbivory, while conversely, the Mexican Hat Flora had a relatively depauperate floral diversity, but exceedingly high levels of insect herbivory (Wilf et al. 2006). It is likely that at finer-grained regional and temporal scales, plant diversity is indeed a driver in the diversity of insect damage, although this can be greatly influenced by climatic factors, ecological disturbance, and depositional environment.

Guidelines for the Study of Ancient Deep Time Plant–Insect Associations

The results of this study are only useful if we evaluate best practices for the study of deep time plant–insect associations. Best practices include:

- Measuring the surface area of each leaf specimen and herbivorized area. Foliar surface area measurements not only documents the intensity of insect

herbivory, which has been found not to necessarily correlate with damage-type diversity (Schachat et al. 2018), but it will also standardize the differences in leaf size. The larger the leaf, the greater the potential for more herbivory, including a greater number of damage types. For example, comparing a palm frond to a legume leaflet in terms of damage-type diversity is grossly imbalanced, but using surface areas for each species allows greater equivalency.

- Additional plant–insect associational studies of Mesozoic Era deposits will be necessary in future meta-analyses (Xiao et al. in review) to achieve significant understanding of the plant–insect fossil record.
- Identifications of fossil angiosperm species or well-resolved morphotypes should include the lowest taxonomic rank possible. We suggest that even when morphotyping, instead of a designation like "Leaf Type 1", if possible and judicious, record with clade- or order-level taxonomic information, (ex. "Magnoliid 1", "Pinales 1", "Malvaceae 1")

Conclusions

Insight into how insect herbivore preferences for plant hosts have changed throughout the age of angiosperms is important to better understand the diversity of plant–insect associations we see today. Although we found that insect preference has changed through geologic time over the past 76 Ma, and in response to the diversity of plants at each locality, these results may instead be indicative of sampling regime

and taxonomic uncertainties rather than broad scale patterns of resource use. These results underscore the need to standardize data collection methods and more carefully consider the results of meta-analyses of plant–insect associations.

Acknowledgments

Thanks to my coauthors, S. Schachat and C. Labandeira, as well as all the authors that shared their datasets. This would not have been possible without the decades of hard work and expertise that provided the building blocks for the study. Thanks also to J. Shultz, for carefully editing this chapter.

Chapter 7: Conclusions

Insects are the most diverse and speciose organisms on earth, and a keystone of modern ecosystems due to the ecological services they provide, including pollination, predation, prey, detritivory, and herbivory. Herbivory in particular has been an important driver of terrestrial ecosystems for hundreds of millions of years and understanding the dynamics of past herbivory will be important in the study of conservation paleobiology (Barnosky et al. 2017, Dietl and Flessa 2011, Dietl et al. 2015, Rick and Lockwood 2013), as well as reconstructing ancient food webs and ecosystems, the end goal for many ongoing collaborative paleontological research projects.

The research presented in this dissertation includes the first quantification of plant–insect associations during the Campanian Age, and is among the relatively few analyses of insect herbivory for the Cretaceous Period. The goals of the dissertation were to document the diversity of insect damage on fossil leaves from the Kaiparowits Formation Flora, describe new plant host species, novel insect damage types, important plant–arthropod associations, and analyze datasets of plant–insect associations during the Age of Angiosperms to better understand large-scale patterns of insect preference of plant hosts. In total, this dissertation documents traces of insect behavior in the Kaiparowits Formation, which has yet to yield recognizable insect body fossils, and explores the role of insect herbivores in ecosystems during the Age of Angiosperms.

Descriptions of fossil plant–insect associations range from ichnotaxonomic descriptions of damage types, to documentation of the earliest known acarodomatia as evidence for a mutualism between plants and mites, and systematic analyses of all types of insect herbivory on *Catula gettyi*, a newly described species of Lauraceae. In addition, a comprehensive analysis of the intensity and diversity of insect herbivores at a single locality within the Kaiparowits Formation details the primary consumption of plants in a Campanian habitat, the JARS locality, and provides a baseline of comparison for future Cretaceous plant–insect associational studies. Finally, deep time plant–insect association datasets are used to test several modern ecological theories of the role that plant–insect associations have on ecosystem productivity. It is anticipated that the results will aid future meta-analyses in our field of study. Avoidable and unavoidable biases in datasets from deep time may complicate even significant results from meta-analyses of ancient ecological datasets, and we need to reevaluate the methodologies we use in this field.

In total, the discoveries and analyses presented in this dissertation allow a better reconstruction of ancient ecosystems of the Kaiparowits Formation, recognize some of the first documented plant–insect associations from a Campanian-aged deposit, and trace the evolutionary trajectories of modern insect lineages and ecological associations back in time to the Late Cretaceous.

Future Directions

After surveying plant–insect associational studies covering a wide range of time periods and geographic localities, I am consistently reminded of the general trends within the field and gaps in our knowledge. There are major unstudied periods

of time in the fossil record where plant–insect associations would benefit from analysis. These include additional, systematic studies on floras that likely contain the earliest evidences of insect herbivory, the Permian/Triassic Extinction Event, and most importantly, a full survey of the Mesozoic. Capturing plant–insect associations before, during, and preceding the rise and radiation of angiosperms is of great importance when studying the coevolution of angiosperms and herbivorous insects. Indeed, several workers are currently researching mid-Cretaceous insect herbivory, but there remains much more work to be done in the broader Mesozoic. The work may be hampered by the relatively small number of known Jurassic and Early to mid-Cretaceous floras, but this is an opportune time to support international paleontological teams that may discover, and control access to, new and important fossiliferous deposits. Furthermore, much of the literature on herbivory studies is from the Northern Hemisphere, notably the Western Interior of North America (i.e. this dissertation) and Europe. Studies from the Southern Hemisphere are disproportionately important (ex. Currano et al. 2011, Donovan et al. 2016, Donovan et al. 2018, Fernández and Chiesa 2020, Liu et al. 2020, Ma et al. 2020, McDonald et al. 2007, Möller et al. 2017, Prevec et al. 2009, Scott et al. 2004, Srivastava and Srivastava 2016, Zhang et al. 2018), and more are needed to counterbalance the Northern Hemisphere biases.

Additionally, for all plant–insect associational studies, sampling regimes should be carefully considered and explicitly stated. If we can create reproducible, comparable datasets, future meta-analyses will be both successful and informative. This includes examination of plant–insect associations for entire floras and trying to

determination of the taxonomic identities of plant hosts. Here I outline goals for my future research and the entire field of study:

1. Collect fossils in a systematic and unbiased way (i.e. census collecting, collecting all plant taxa present).
2. Increase sample sizes if possible. No matter the sample size, subsample and rarefy the data to make comparisons less biased.
3. Use the Labandeira et al. (2007c) *Guide to insect (and other) damage types on compressed plant fossils (version 3.01)* and the forthcoming *Version 4*, to describe insect damage on fossil leaves and contribute to the guide with new damage types. This is a communal resource that is constantly updated by researchers from across the globe. Ichnotaxonomic descriptions of damage type can be useful (see Chapter 3), but these descriptions are best undertaken when the damage is identifiable to a particular insect herbivore lineage.
4. Measure surface area of leaves and insect damage. This methodology takes a great deal of time, but it standardizes data to account for differences in leaf size. For example, a palm leaf and a legume leaflet have different potentials for the intensities and diversities of insect damage. Moreover, diversity of herbivory and intensity of herbivory are not necessarily correlated, so surface area measurements capture an important metric of insect herbivory that leaf count and damage type diversity cannot.
5. Publish datasets and consider publishing data on your own if the journal does not support data publication.

6. Try to publish in open access journals, and if not feasible, use online platforms to make research available and/or be responsive to online requests for publications.
7. Test hypotheses regarding how land plants became herbivorized during the past 400 million years, and describe the modes, mechanisms, and consequences of the evolution of insect herbivory.

I greatly look forward to the future of research on deep time plant–insect associations, hopefully produced by an even more diverse pool of scientists, studying new time periods, geographic areas, and implementing novel and visionary analyses.

Appendices

A. Letter to the Dean of the Graduate School

To Dr. Steve Fetter, Dean of the Graduate School:

Sarah Augusta Maccracken, a Ph.D. candidate in the Department of Entomology (College of Computer, Mathematical, and Natural Sciences), wishes to include the following publication in her dissertation, "Plant–Arthropod Associations from the Western Interior of North America During the Late Cretaceous"

Maccracken, S. A., I. M. Miller, and C. C. Labandeira. 2019. Late Cretaceous domatia reveal the antiquity of plant–mite mutualisms in flowering plants. Biology Letters 15(11):20190657.

We, the examining committee of Sarah Augusta Maccracken, have determined that she made a substantial contribution to the aforementioned publication, as per the guidelines set forth in the graduate catalogue for the inclusion of one's own previously published materials in a dissertation. The inclusion of this work in her dissertation has the approval of her dissertation committee, dissertation advisors Dr. Jeffrey Shultz (Graduate Director of the Department of Entomology) and Dr. Conrad Labandeira.

Signature: Jeffrey W Shultz	Date: 10/12/20	Advisor
Signature: Conrad Labandeira	Date: 2020-10-22	Advisor
Signature: Charles Delwiche	Date: 2020-10-13	Committee Member
Signature: Dan Gruner	Date: 2020-10-22	Committee Member
Signature: Ian Miller	Date: 2020-10-22	Committee Member
Signature: Jeffrey W Shultz	Date: : 10/12/20	Director of Graduate Studies, Entomology

B. Chapter 2 Supplementary Information

Modern Insect Herbivory on Lauraceae

Although all herbivore functional feeding groups provide a variety of damage types on extant members of the Lauraceae, there are some notable patterns of herbivory within the family. The DTs inflicted by hole, margin and surface feeders, as well as skeletonizers, are at typical levels of diversity expected for a moderately diverse host-plant family such as Lauraceae. However, a considerable proliferation of associations exists between the broad taxonomic varieties of scale insects and particular host species of Lauraceae. By contrast, the frequency of leaf miners on Lauraceae are minimal (Spencer 2012), while gallers are very diverse, particularly in the Neotropics (Maia et al. 2014). Seed predation is overwhelmingly accomplished by small vertebrates rather than insects (Martins et al. 2015, Myster 1997). Several ant–plant associations, such as between the sweetwood hosts *Ocotea dendrodaphne* Mez and *O*. *atirrensis* Mez & Donn that house the ant symbiont *Myrmelachista flavocotea* Longino, have been documented (McNett et al. 2010). Another ant–plant association is between *Ocotea pedalifolia* Mez and the ant *Myrmelachista* sp. as before, but involving a third mutualist member, the mealy bugs *Dysmicoccus brevipes* (Cockerell) and *D*. *cryptus* (Hempel) that also live in the hollowed-out stems (Stout 1979).

Hole Feeding. — The polyphagous beet armyworm *Spodoptera exigua* Hubner (Lepidoptera: Noctuidae) is a prominent hole feeder on *Lindera benzoin* L. (spicebush) in the Southeastern United States. This generalist herbivore, however,

lessens its levels of hole feeding under conditions of induced response in which its plant host responds to herbivore attack by producing feeding-deterrent substances and structural defenses in foliar tissues (Mooney et al. 2009).

Margin Feeding. — The specialist herbivore, *Epimecis hortaria* F. (Lepidoptera: Geometridae) is a major margin feeder on *Lindera benzoin* L. and *Sassafras albidum* (Nuttall) Nees. This relationship is particularly striking, as elevated levels of photoprotective phenolic compounds occur in sun leaves where higher temperatures increase photosynthesis (Niesenbaum and Kluger 2006), resulting in decreased nitrogen levels. Feeding *E. hortaria* larvae respond by increasing significantly their level of herbivory (Mooney and Niesenbaum 2012). By contrast, shade leaves on the same plant display decreased levels of *E*. *hortaria* margin feeding. although this pattern is not true for all herbivores (Niesenbaum 1992). The Promethea Silkmoth, *Callosamia promethea* (Lepidoptera: Saturniidae), is a large caterpillar that feeds on *Sassafras albidum* as one of its primary hosts, also preferring sun leaves over shade leaves (Osier and Jennings 2007).

Skeletonization. — Although recently introduced from Japan, the highly polyphagous Japanese beetle *Popillia japonica* (Coleoptera: Scarabaeidae) is probably the most prolific skeletonizer of lauraceous sassafras, *Sassafras albidum*, native to Eastern North America (Potter and Held 2002). Other than the Japanese beetle, there are few native skeletonizing insects on Lauraceae.

Surface Feeding. — Several species of the specialist skipper genus *Venada* (Lepidoptera: Hesperiidae) are apparently obligate surface feeders of several species

of the aromatic, lauraceous *Ocotea* (sweetwood) (Burns et al. 2013). The feeding damage of *Venada* produces light-colored, polygonal patches of removed epidermal leaf tissue. The most conspicuous obligate surface feeder on Lauraceae is the Spicebush Swallowtail, *Papilio troilus* L. (Lepidoptera: Papilionidae), that feeds on members of Lauraceae in Eastern North America such as *Lindera benzoin*, *Sassafras albidum*, its two primary hosts, and *Cinnamomum camphora* L. J. Presl. (camphor), *Persea borbonia* L. (Spreng.) (Redbay), and occasionally members of more distantly related Magnoliaceae (Nitao et al. 1991).

Piercing and Sucking. ― The numerous relationships between piercing-and-sucking scale insects and planthoppers on modern Lauraceae hosts indicate that piercing and sucking harbors the single most diverse functional feeding group for Lauraceae. Almost all of these common hemipteran associations are polyphagous and target vascular phloem tissue, such as the black scale, *Saissetia oleae* (Bernard) (Coccidae), on California bay *Umbellaria californica* (Hook. & Arn.) Nutt. in California. The similarly polyphagous cottony cushiony scale, *Iceyra purchasi* Maskell (Monophlebidae), is found on bay laurel *Laurus nobilis* L., as is the planthopper, *Metcalfa pruinosa* (Say) (Flatidae), also occurring on *L. nobilis*. The palm fiorina scale, *Fiorinia fioriniae* Targioni-Tozzetti (Diaspididae), is a worldwide pest on species of *Persea*, particularly avocados, in California and Florida, although palms are the preferred host. Piercing-and-sucking insects produce damage on their host plants characterized as cratered punctures and circular, elliptical or ovoidal impressions on surface tissues (Johnson and Lyon 1991).

Oviposition. — Many Lepidoptera, such as papilionid butterflies, oviposit on the leaf surfaces of a variety of lauraceous hosts that often are food plants for their larvae (Carter and Feeny 1999, Frankfater and Scriber 1999). However, these oviposition events do not leave detectible damage on epidermal tissue and would not enter the fossil record. There are few instances of documented oviposition that produce recognizable scar tissue on extant Lauraceae. One example is the damselfly *Palaemnema desiderata* Selys (Odonata: Platystictidae) ovipositing on the twigs, branches and leaf petioles of the lauraceous *Licaria* sp. in Panama (Soriano et al. 1982).

Mining. — Lauraceae hosts are poorly represented among leaf-mining insects. The most prominent leaf-miner family on Lauraceae (Labandeira et al. 2002a, Labandeira et al. 2002b) are the gracillariid genera *Acrocercops*, *Caloptila*, *Gracillaria*, *Lithocolletis* and *Phyllocnistis* that occur on *Cinnamomum*, *Laurus*, *Lindera*, *Litsea*, *Persea*, *Sassafras* and *Umbellaria* (Fletcher 1920, 1933, Hering 1957, Kumata 1982, Kumata et al. 1988, Needham et al. 1928, Yuan and Robinson 1993). Documented occurrences of the Yellow Poplar Weevil, *Odontopus calceatus*, also termed the Yellow Poplar Weevil and Sassafras Weevil (Coleoptera: Curculionidae), mines *Liriodendron tulipifera* L., its primary host, but also mines less commonly *Sassafras albidum* (Nuttall) Nees and introduced *Laurus nobilis* L. in Florida (Buss 2006). The apple leaf miner, *Lyonetia clerkella* L. (Lepidoptera: Lyonettidae), occasionally occurs on *Laurus nobilis*, although its primary host are Rosaceae and birch across Eurasia and Northern Africa (Berg 1960). Although no leafmining flies (Diptera:

Agromyzidae) are miners of Lauraceae, at least 13 genera of Lauraceae host at least four *Phytobia* species of cambium miners in stems and trunks (Spencer 2012).

Galling. — The most notable, described gall association is the avocado psyllid *Trioza anceps* Tuthill (Hemiptera: Psyllidae) on avocado, *Persea americana* L., in the southeastern United States. The incidence of this leaf-curl gall is dependent on the specific chemical profile of its host plant, preferring the variety *drymifolia* within populations of *P. americana* (Torres-Gurrola et al. 2011). Another *Trioza* induced gall occurs on *Nectandra salicina* in Costa Rica, resulting in malformation of a pedunculated fruit that becomes enlarged and is sessilely positioned at the base of a twig (Blackmer and Hanson 1997). One of several Cecidomyiidae (gall midge) galls on Lauraceae is *Pseudasphondylia neolitseae* (Diptera: Cecidomyiidae), a conical foliar gall on *Neolitsea seriacea* (Blume) Koidz. in southern Kyushu, Japan (Yukawa and Akimoto 2006). Nevertheless, the greatest diversity of galls on Lauraceae are present in the Neotropics (Maia et al. 2014). Hosts include *Cinnamomum* (cinnamon), *Cryptocarya* (mountain laurel), *Nectandra* (sweetwood), *Ocotea* and probably unaffiliated genera (Julião et al. 2014, Maia et al. 2014, Medianero et al. 2014).

Seed Predation. — Seeds of Lauraceae are overwhelmingly large and typically are dispersed and occasionally predated by birds and small mammals (Holl and Lulow 1997, Martins et al. 2015). Insect predation on seeds of Lauraceae is rare and typically affect species with smaller seeds. One example is loblolly sweetwood *Ocotea leucoxylon* (Sw.) Laness. occurring on landslides within forests in Puerto Rico, that are predated by undisclosed insects (Myster 1997). The large, robust fruits of many species of *Persea* (bay, avocado) that are distributed in the Neotropics have a

dispersal syndrome favoring intact consumption and dispersal of the large seeds by mammal megaherbivores that became extinct during the end of the Pleistocene Epoch (Wolstenholme and Whiley 1999). The extinction of browsing and seed-dispersing megaherbivores such as litopterns, ground sloths, gompotheres and New World horses rendered many modern species of *Persea* as "neotropical anachronisms" that presently lack the facility of seed dispersal (Janzen and Martin 1982).

5.2.10. Pathogens. — Laurel wilt is a vascular disease that invades the xylem of many species of Lauraceae. The disease caused by *Raffaelea lauricola* T.C. Harr (Ascomycetes: Ophiostomataceae) and is vectored by the ambrosia beetle *Xyleborus glabratus* Eichoff (Coleoptera: Curculionidae), which is especially harmful to *Persea borbonia* of the Southeastern United States (Hughes et al. 2015).

Tritrophic Interactions. — When generalist (polyphagous) lepidopteran larvae of Arctiidae and Megalopytidae that consumed secondary compounds of *Necandra hypoleuca* and *N. latifolia*, respectively, were in turn consumed by the adult ant *Paraponera clavata*, there was a minimal rejection rate of the larval prey items (Dyer 1995). However, when specialist (monophagous) lepidopteran larvae of Lasiocampidae, Nymphalidae and Saturniidae consumed *N. hypoleuca*, *Ocotea meziana* and *Ocotea* sp., respectively, there was an elevated rejection rate of the larval prey items. This study indicates that specialist lepidopteran larvae feeding on certain species of Lauraceae can sequester and concentrate secondary compounds to the detriment of predators such as an ant.

Antiherbivore Resistance in Modern Lauraceae

Modern Lauraceae contain significant levels of secondary compounds. For example, *Persea americana* Mill. (avocado) foliage is especially rich in monoterpenes, sesquiterpenes and similar compounds (Niogret et al. 2013) in the Southeastern United States. In Eastern North America *Lindera benzoin* has low levels of herbivory particularly in sun rather than shade environments due to production of the phenols of vanillic, chlorogenic, *p*-coumaric and ferulic acids (Ingersoll et al. 2010). Monoterpenes occur at modest levels at all developmental stages of California bay, *Umbullaria californica* (Hook. & Arn.) Nutt, where it apparently is a deterrent to folivorous insects and blacktail deer (Goralka and Langenheim 1996), but prized as adding flavor and aroma to cooked foods. However, at the Miyazaki Experimental Forest in Japan, foliar extracts of 16 lauraceous species of *Actinodaphne*, *Cinnamomum*, *Laurus*, *Lindera*, *Litsea* and *Machilus* proved to have negative consequences when fed to insects (González-Coloma et al. 1994a, González-Coloma et al. 1994b). The outcomes of these extracts ranged from subtle antifeedent effects to toxins causing death (González-Coloma et al. 1994a, González-Coloma et al. 1994b).

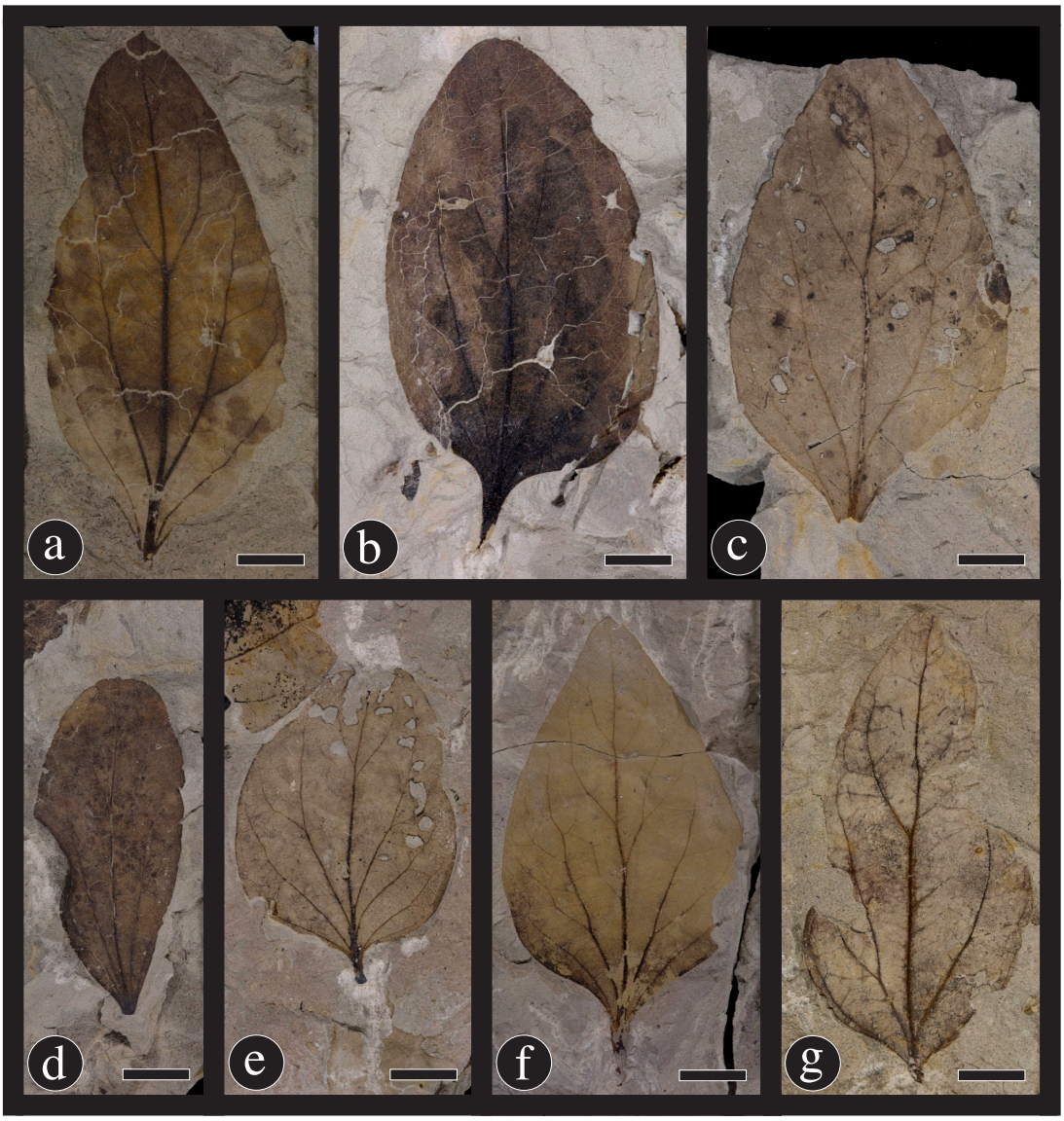
An interesting occurrence in the Canary Islands of Spain features a highly defended laurel forest, where *Appolonia barbusana*, *Laurus azorica*, *Ocotea foetens* and *Persea indica* exhibit elevated levels of cyanoid diterpenes that have varying levels of insecticidal properties (González-Coloma et al. 1994a, González-Coloma et al. 1994b). Cyanoid dipertene plant extracts of cyandol, cyanoids and cinnceylanol from the four lauraceous genera exhibited modest antifeedent properties to strong growth inhibition when fed to larvae of the lepidopteran tobacco cutworm *Spodoptera*

litura F. (Noctuidae), cotton bollworm *Heliothis armigera* Hübner (Noctuidae) and tussock moth *Calliteara fortunata* Rogenhofer (Erebidae), as well as the Japanese termite *Reticulitermes speratus* (Kolbe) (Isoptera: Rhinotermitidae) (González-Coloma et al. 1994a, González-Coloma et al. 1994b). The moderate to strong insecticidal properties of extracts from these four lauraceous species suggest a collective response to insect herbivory in a geographically constrained, insular environment. Interestingly, in a DNA–bar-coding study of a rainforest dominated by Dipterocarpaceae and from the much larger island of Borneo, species of the leaf beetle *Anadimonia* that were specialized on two species of Lauraceae displayed low levels of feeding, indicating high levels of chemically-defended lauraceous foliage (Kishimoto-Yamada et al. 2013).

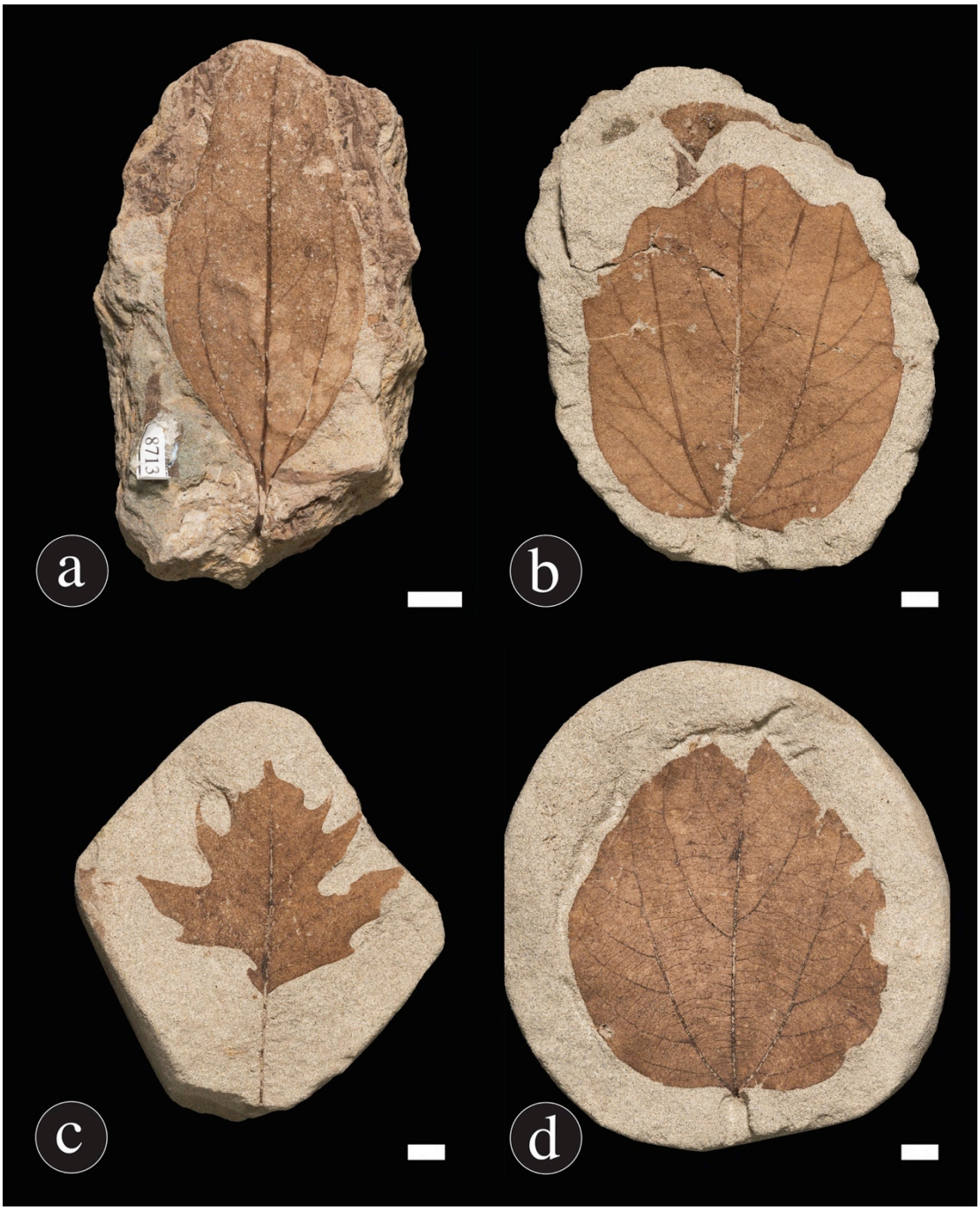
In addition to chemical defenses, Lauraceae possess considerable structural defenses. Features frequently found in Lauraceae indicate mechanical impediments to insect herbivory principally involve leaf toughness (Grubb 1986). Elements contributing to leaf toughness are thickened epidermis layers, cell-wall rigidity in hypodermis layers, and the presence of robust, girdling fiber strands (Grubb 1986). Recently, the report of cork warts on the leaves of six species of *Mezilaurus* indicates a novel type structural defense in Lauraceae (Vaz et al. 2018). Cork warts are accumulations of suberized, thickened cells surrounding smaller, radially arranged epidermal cells (Vaz et al. 2018), and provide an additional level of antiherbivore structural defense.

Supplementary Table 2.1: Comparable species to *Catula gettyi*.

Species epithet
Cinnamomum palaciosii
Cinnamomum hatschbahii
Cinnamomum litsaeaefolium
Cinnamomum halmaheirae
Cinnamomum pedatineruium
Cinnamomum australe
Cinnamomum glaziovii
Cinnamomum tomentulosum
Cinnamomum chana
Cinnamomum camphora
Cinnamomum montanum
Cinnamomum zapatae
Cinnamomum erythropus
Cinnamomum taubertianum
Cinnamomum pedunculatum syn. japonicum

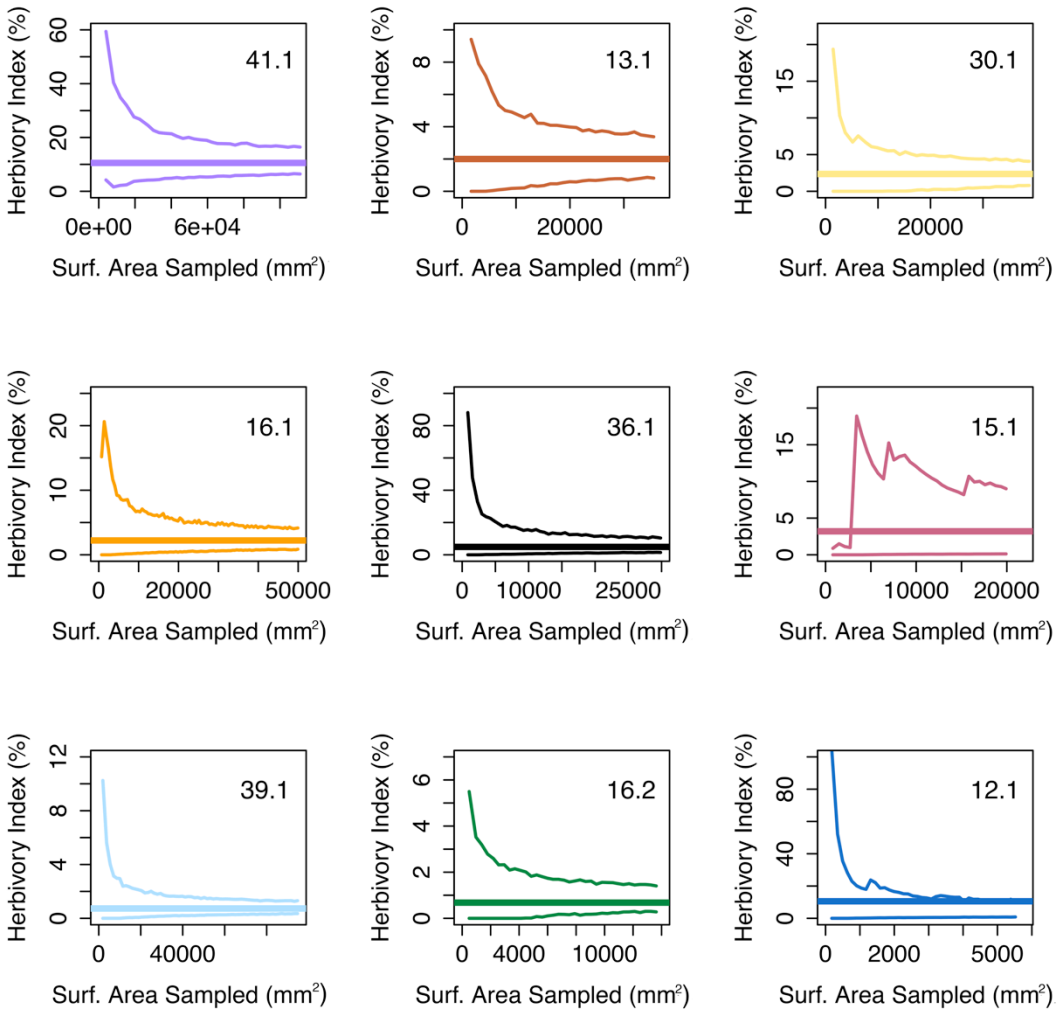


Supplementary Figure 2.1: Paratypes of *Catula gettyi* showing the range of leaf architecture exhibited by this taxon. (a) DMNH 41570. (b) DMNH 54371. (c) DMNH 54379. (d) DMNH 54370. (e) DMNH 41584. (f) DMNH 41567. (g) DMNH 54380. Scale bars = 1.0 cm.



Supplementary Figure 2.2: Hell Creek species: (a) *Marmarthia pearsonii*, (b) *M. trivialis* (c) "*Artocarpus*" *lessigiana,* and (d) "*Ficus*" *planicostata*. Black scale bars= 10 mm; white scale bar= 10 mm. Photographs by R. Wicker, DMNS.

C. Chapter 3 Supplementary Information



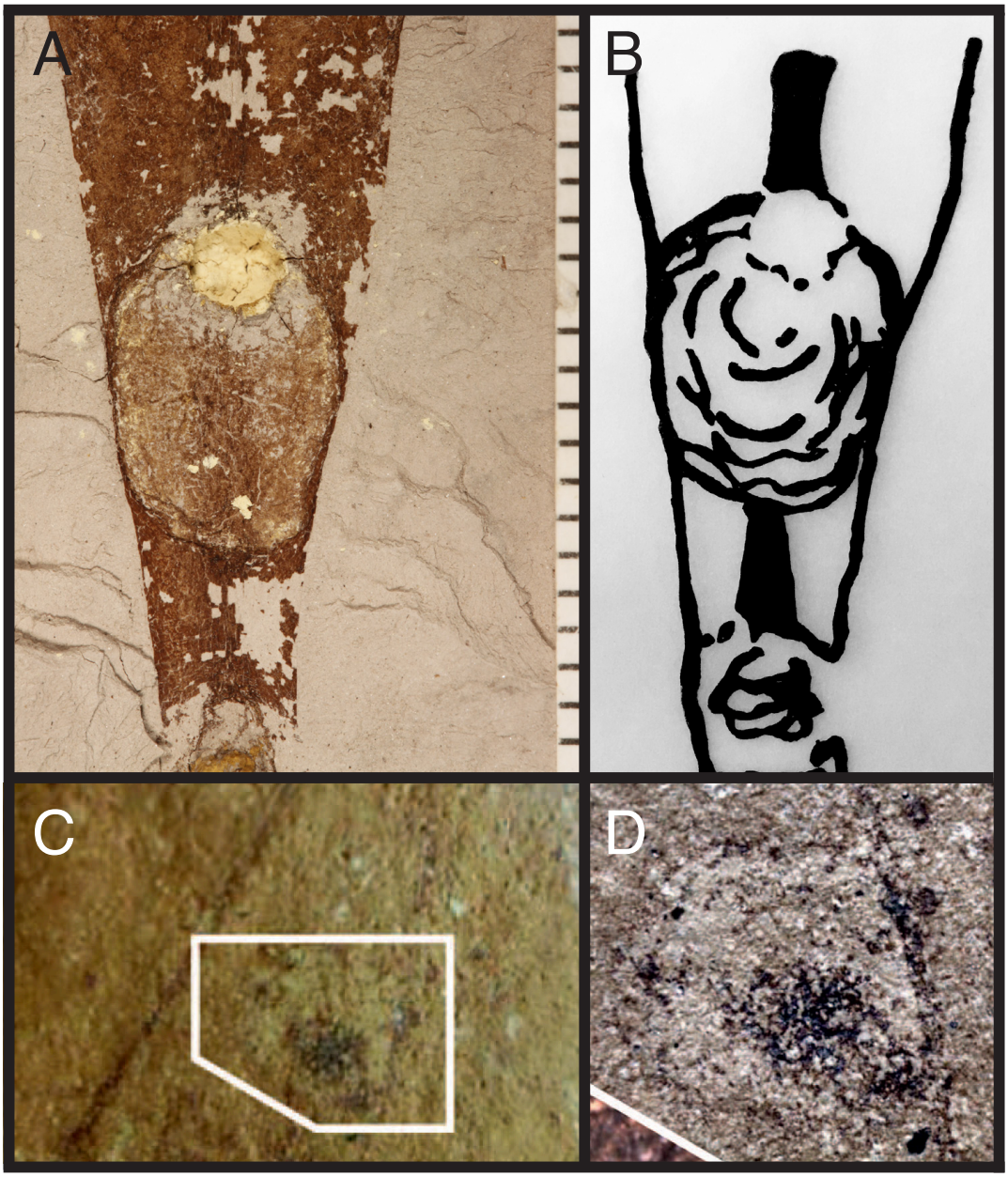
Supplementary Figure 3.1: Herbivory index for individual plant hosts in the JARS locality. Center line represents the herbivory index and the upper/lower boundaries represent the 95% confidence interval range.

D. Chapter 4 Supplementary Information

Locality Description of Fossil Leaf Morphotype KP90 that bears *Leucopteropsis spiralis*

The leaf morphotype KP90 occurs as isolated leaves. Leaf attachment petiolate; leaf organization presumed simple. Petiole terete, flanked with a thin wing of laminar tissue extending from the blade, wing width ~0.2 mm or less; petiole base slightly swollen with a C-shaped base interpreted as an abscission scar. Blade attachment marginal. Laminar size notophyll to mesophyll; laminar length 6.5 to 13 cm; laminar width 1.2 to 3.1 cm; laminar length to width ratio 4:1 to 6:1. Laminar shape oblong, or slightly elliptic in smaller specimens; medial symmetry typically symmetrical, slight asymmetry in ~25% of the specimens. Laminar base asymmetrical, with an asymmetrical basal insertion; base angle acute; base shape rounded to convex. Laminar apex angle acute; apex shape convex to rounded; laminar apex without specialized features. Leaf margin entire, unlobed, and with a slight marginal undulation in most specimens; laminar edge otherwise appearing unremarkable. Laminar surface texture appearing smooth. Primary venation pinnate; course of primary vein straight; primary vein much thicker (> 10x) than secondary veins. Secondary vein organization simple brochidodromous; agrophic veins absent; naked basal veins absent; spacing of secondary veins on primary vein varies between regular and irregular; angle of secondary vein departure from primary vein acute and uniform; attachment excurrent; major secondary veins occasionally anastomose as they approach the leaf margin. Minor secondary veins absent. Intersecondary veins present; extending < 50% of the length of the subjacent secondary vein; proximal

course parallel to major secondary veins, distal course reticulating; frequency of < 1 intersecondary vein per intercostal area. Intercostal tertiary vein organization opposite percurrent and sinuous; tertiary vein course angle with respect to the primary vein obtuse; tertiary vein angle variability with respect to the primary vein inconsistent. Epimedial tertiary veins reticulate; proximal course parallel to the subjacent secondary vein; distal course parallel to the intercostal tertiary vein. Exterior tertiary course looped. Quaternary vein fabric irregular reticulate. Quinternary vein fabric irregular reticulate. Areolation appearing to exhibit poor development, however, higher order venation generally not preserved; freely-ending veinlets not observed. Marginal ultimate venation exhibiting incomplete loops. No cuticular or fertile material recovered or associated with these leaf fossils.



Supplementary Figure 4.1: (a) Photograph of *Tischeria* sp. leaf mine (Specimen no. IU15808-7545, Mine type KLm14) from the Maastrichtian of the Tennessee (Ripley Formation) and (b) redrawn illustration from Stephenson (1992) (Sohn et al. 2012, Stephenson 1992). (c) A blotch leaf mine from the Miocene San José Formation of Argentina (Specimen no. CTES-IC 176, new damage type) and (d) close up, used with permission from Robledo (Robledo et al. 2018).

E. Chapter 5 Supplementary Information

Locality Description

During the past 10 years of field exploration, more than 100 megafloral localities have been found and collected in the ca. 860 m thick, Campanian-aged Kaiparowits Formation (76.6 – 74.5 Ma) (Roberts et al. 2013) in southern Utah, USA (Supplementary Figure 5.1). Most of these localities occur in the middle member (ca. 90-110 to ca. 550 m) (Roberts 2007) of the formation. Within the middle member, the majority of megafloral localities are further restricted to the stratigraphic zone between ca. 300 and 450 m. The fossil leaf species presented in Maccracken et al. (main text) that hosts the mite domatia is designated as plant morphotype "KP88" (the morphotype number is an abbreviation for the Kaiparowits Formation [KP] and a sequential listing of the number of morphotypes in the formation (see Miller et al. 2013)). The host taxon, KP88, occurs at only two localities: DMNH Loc. 3725 (JARS) and 4000 (Talk Radio), which occur at ca. 365 ± 20 m and ca. 440 ± 10 m above the base of the formation, respectively (Supplementary Figure 5.2). A depositional rate of 41 cm/1,000 years was obtained by calculating $^{40}Ar/^{39}Ar$ ages on sanidine crystals from volcanic ash beds (Roberts et al. 2013) and informs our dating of the acarodomatia. Considering only the error associated with the stratigraphic position of the localities, we estimate the age of DMNH locality 3725 at 75.7 ± 0.05 Ma and DMNH locality 4000 at 75.5 ± 0.02 Ma. These dates are equivalent to a late Campanian age (Walker et al. 2013).

The two localities at which morphotype KP88 occurs represent different depositional environments. In the facies association (FA) classification of Roberts

(2007) for the Kaiparowits Formation, DMNH locality 3725 (Roberts et al. 2013) occurs in FA6, which is finely laminated, calcareous silt- and mudstone. This facies association is interpreted as forming in lacustrine settings (Roberts 2007). In contrast, DMNH locality 4000 occurs in FA5, which is minor tabular and lenticular sandstone, immediately above FA9, which is carbonaceous mudstone. FA5 is interpreted as forming in crevasse splays and crevasse channels, and FA9 is interpreted as forming in swamps and oxbow lakes (Roberts 2007).

Currently, KP88 is represented by 41 partial specimens: 34 from DMNH locality 3725, and 7 from DMNH locality 4000. Acarodomatia (13 total) are found on ten specimens: EPI. 40928, 40929, 40930, 40931, 40932, 40933, 45427, 45455, 45456, and 47132.

The very large size of this fossil leaf morphotype, exceeding 30 cm in length and 25 cm in width, likely led to pre- and post-depositional lamina fragmentation and the omnipresence of partial specimens in the settings for which it is found. Until more complete material is recovered, we elect to describe KP88 while retaining its informal morphotype designation.

Leaf Description

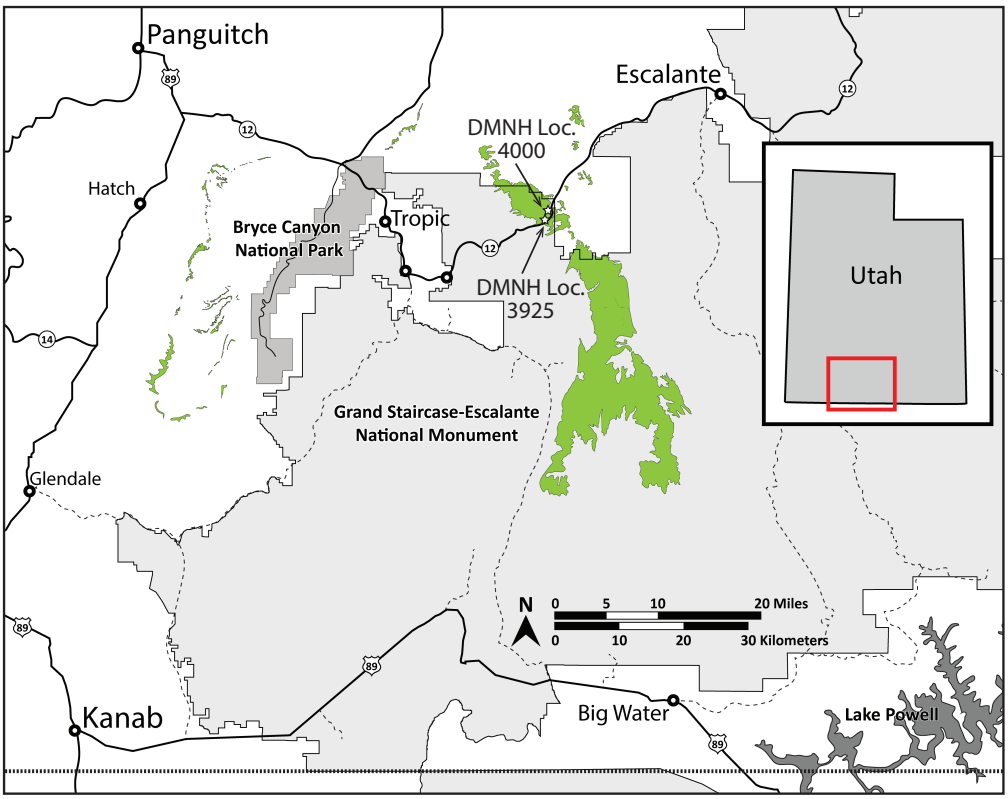
The following terminology used follows Ellis et al. (2009) (Ellis et al. 2009). Leaves likely simple. Leaf attachment appearing petiolate; arrangement with other leaves unknown. Petiole exhibiting a pronounced corrugated texture; up to 1 cm thick; alternatively, leaves could be nearly sessile and attached to a woody and corrugately textured branch. Blade attachment marginal. Lamina of megaphylly size; length exceeding 30 cm; width exceeding 25 cm; and a lamina length to width ratio

ca. 1.2:1. The lamina shape appearing ovate; medial lamina slightly asymmetrical. Laminar base appearing symmetrical; base angle reflexed; base shape cordate. Lamina apex not observed. Leaf margin entire (untoothed), unlobed; laminar surface texture appearing smooth (small raised bumps on the compression/impression surface are interpreted as mineral deposits). Primary venation pinnate; thickness of primary vein up to ca. 0.5 cm; course of primary vein more or less straight; primary vein decreases in width toward apex after giving rise to major secondary veins; on some specimens it appears that laminar tissue partially covers the primary vein, particularly near the leaf base. Secondary vein organization appearing simple brochidodromous; agrophic veins present, simple; seven basal veins present including both primary and secondary veins; naked basal veins absent; secondary veins immediately crowded at the leaf base but otherwise regularly spaced along the primary vein; angle of secondary vein departure from primary vein acute and constant; secondary vein course appearing to arch towards the leaf apex, decurrent on the primary vein; minor secondary veins absent (with the exception of the agrophic veins); interior secondary veins and intersecondary veins absent. Intercostal tertiary vein organization preserved in small portions of the recovered leaf material; where observed, alternate percurrent and sinuous; tertiary vein course angle with regard to the primary vein obtuse; tertiary vein angle variability unknown. Epimedial tertiary veins appearing alternate percurrent; proximal course perpendicular to the midvien, distal course unknown. Exterior tertiary course unknown. Quaternary and higher vein fabric unknown. Highest order veins observed along marginal venation, appearing looped. No cuticular or fertile material has been recovered or associated with these leaf fossils.

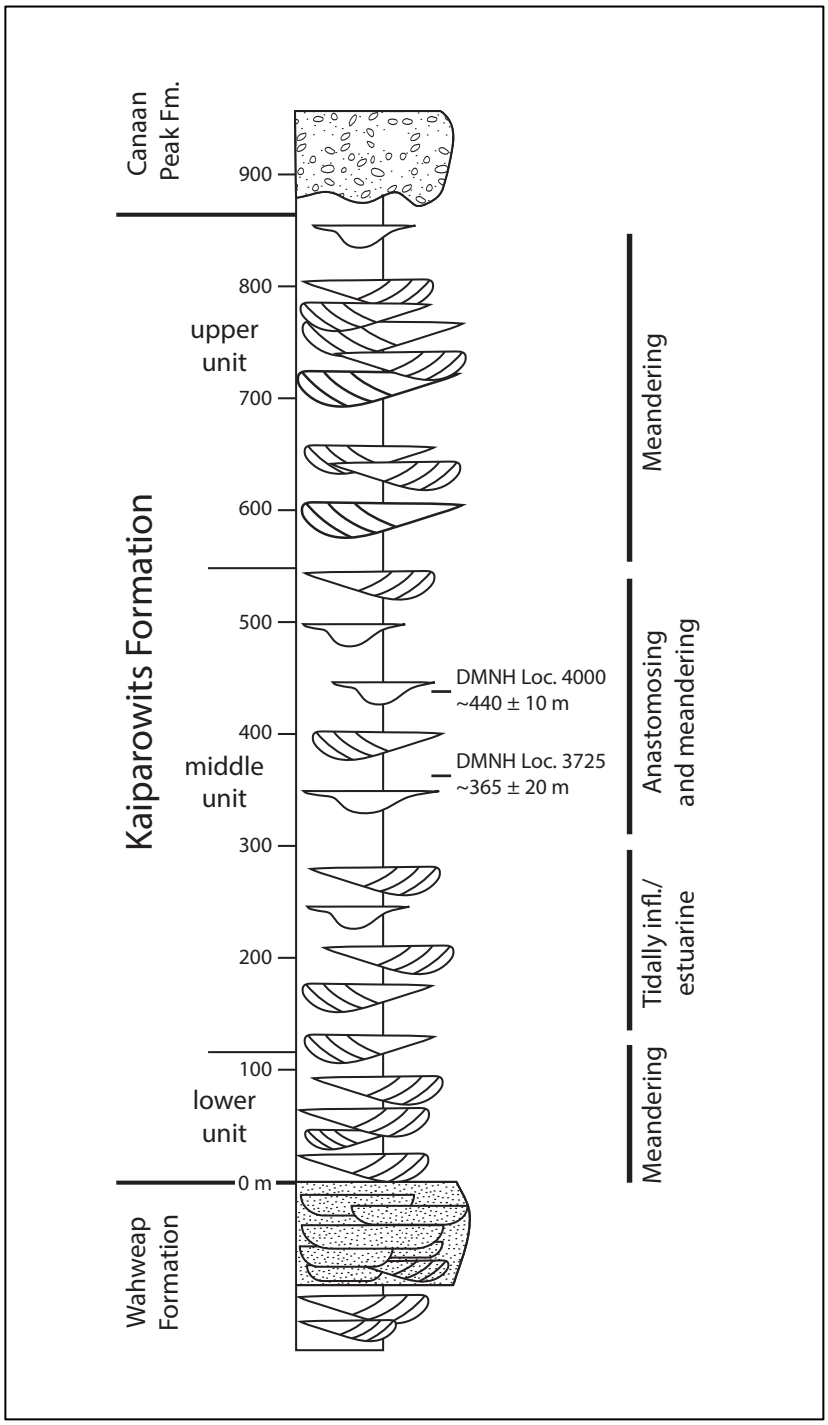
Morphotype Exemplar. DMNH EPI.47131 (Supplementary Figure 5.3 A–C).

Referred Specimens (not figured). DMNH 40928, 40929, 40930, 40931, 40932, 40933, 45427, 45455, 45456.

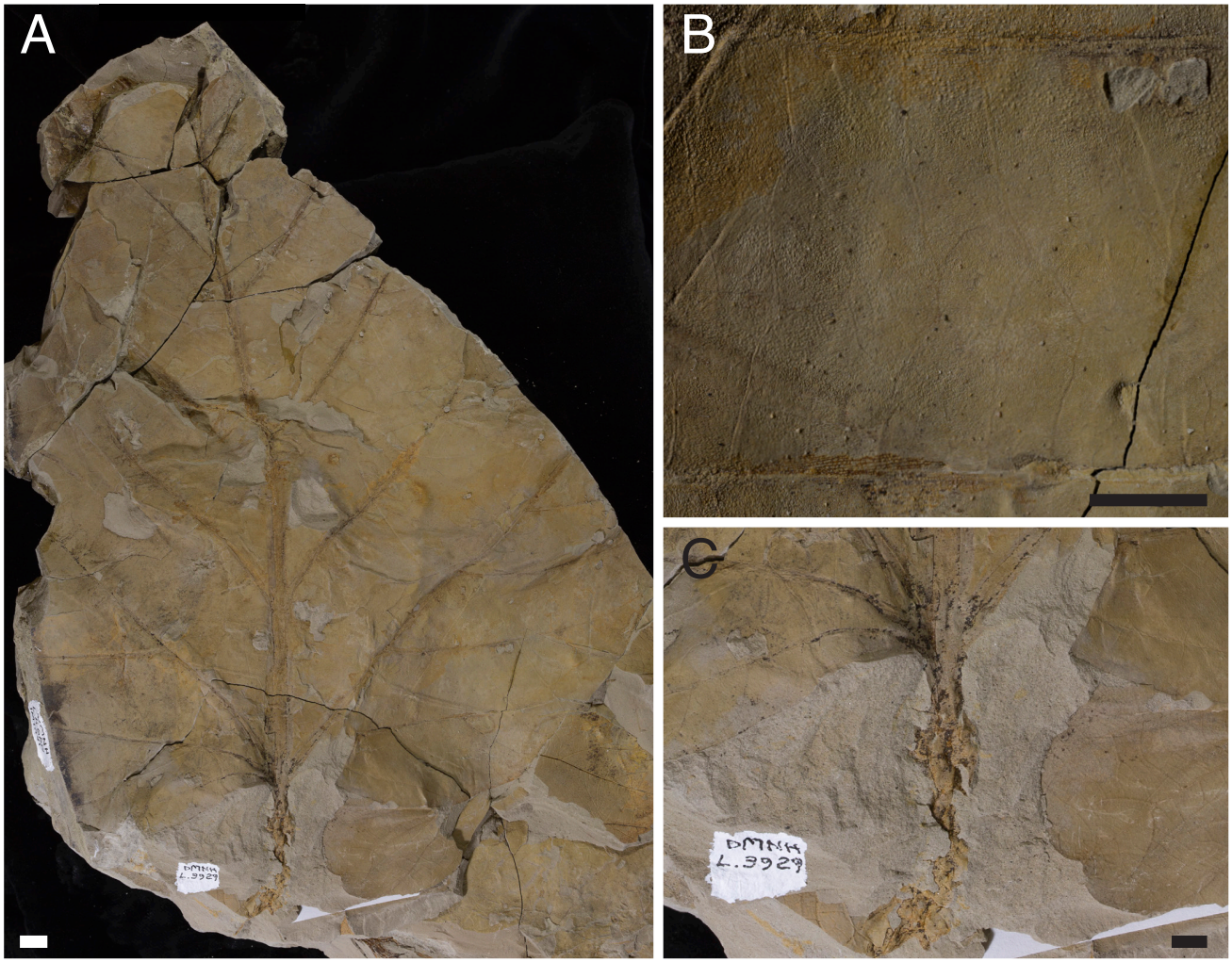
Damage Type (DT) Assignment. This acarodomatium is assigned to DT339 in an addendum to the most recent version of the *Damage Guide* (Labandeira et al. 2007c).



Supplementary Figure 5.1: Map showing major roads, towns and land designation boundaries in southern Utah, USA. The exposures of the Upper Cretaceous Kaiparowits Formation are shown in green. Stars indicate the approximate locations of DMNH localities 3725 and 4000 where KP88 was found. Figure modified from Lyson et al. (2017).



Supplementary Figure 5.2: Representative stratigraphic column for the Kaiparowits Formation redrawn from Roberts (2007) showing major sedimentary modes. The stratigraphic positions are shown of DMNH localities 3725 and 4000 where examples of KP88 were recovered.



Supplementary Figure 5.3: Morphotype exemplar specimen DMNH 47132 of KP88 described in Maccracken et al. (2019) from DMNH locality 4000. (a) The most complete specimen of KP88. Specimen shows about 75% of the lamina. (b) Detail showing the lower right-hand section of the leaf with alternate percurrent tertiary vein fabric. The large veins at top and bottom of the image are secondary veins. (c) Detail showing corrugated surface on petiole or stem. White scale bar = 1.0 cm; black scale bars = 0.5 cm.

G. Chapter 6 Supplementary Information

The Fruitland and Kirtland Formations

The Fruitland and Kirtland (F/K) Formations are located in the northwest corner of New Mexico, USA, at approximate paleolatitude of 44.2^{o}N (Miller et al. 2013). These formations are among the upper units within the San Juan Basin, bounded by the older Pictured Cliffs Sandstone and a massive uncomformity that separates the Cretaceous strata from the overlaying Tertiary Ojo Alamo Sandstone (Fassett and Steiner 1997, Hunt and Lucas 1992). Radiometric dating of volcanic ash by Fassett and Steiner (1997) found the Fruitland/Kirtland Formations to be middle Campanian in age (ca. 73–75.5 Ma).

The F/K Formations are well-known for fossils of vertebrates, invertebrates, and plant macrofossils (Davies-Vollum et al. 2011, Hunt 1991, Hutchinson and Kues 1985, Longrich 2011, Sullivan 1999, Sullivan and Lucas 2006, Sullivan and Lucas 2000, Sullivan and Williamson 1999, Williamson 2000, Williamson and Weil 2008). The Kirtland Formation overlies the older Fruitland Formation, but they are often grouped together owing to similar depositional environments (Fassett and Steiner 1997, Hunt and Lucas 1992). In general, fossils are found in fine-grained and organic deposits, which are interpreted as floodplains and overbank deposits or in slightly coarser-grained rocks that were likely channel systems (Davies-Vollum et al. 2011, Hunt and Lucas 1992). Fossil leaves in the F/K Formations are found in fine-grained mudstones and sandstones. Formal descriptions of all localities will be made available in future paleobotanical publications.

Fruitland/Kirtland Formations specimens are housed at the National Museum of Natural History in Washington, DC. This flora was collected by Dr. Lisa Boucher and colleagues from 1999–2004.

Supplementary Table 6.1: Plant hosts with significantly higher levels of insect herbivory than expected and all relevant associated data.

Species/ Morphotype	Locality	Publication	Abun-dance Rank	p-value	Pterido-sperm	Gymno-sperm	Angio-sperm	ANA-Grade	Mag-nolii d	Mono-cot	Eu-dicot	N-Fixer	Age (Ma)
Vitis sp.	Bernasso	Adroit et al. (2016)	12	0.006	0	0	1	0	0	0	1	0	2
Tilia saportae	Willershausen	Adroit et al. (2018)	51	0.001	0	0	1	0	0	0	1	0	2.8
Fraxinus ornus	Willershausen	Adroit et al. (2018)	78	0.003	0	0	1	0	0	0	1	0	2.8
Betula cristata	Mókollsdalur	Wappler & Grímsson (2016)	2	0.009	0	0	1	0	0	0	1	0	8.5
Quercus rhenana	Břešťany	Knor et al. (2012)	8	0.000	0	0	1	0	0	0	1	0	19.6
Populus zaddachii	Bílina	Knor et al. (2012)	20	0.000	0	0	1	0	0	0	1	0	19.6
cf. *Berberis* sp.	Level NH	Domínguez (2018)	4	0.007	0	0	1	0	0	0	1	0	25.4
Type K1	CH72	Currano et al. (2011)	2	0.003	NA	NA	NA	NA	NA	NA	NA	NA	27.5
Plant Host 19	323	Wilf et al. (2001)	3	0.006	NA	NA	NA	NA	NA	NA	NA	NA	43
Plant Host 12	1732	Wilf et al. (2001)	4	0.005	NA	NA	NA	NA	NA	NA	NA	NA	43
Plant Host 15	1732	Wilf et al. (2001)	9	0.001	NA	NA	NA	NA	NA	NA	NA	NA	43
Laura Sp.	Eckfeld	Wappler et al. (2012)	10	0.000	0	0	1	0	0	0	0	0	44.3
Ulma Sp.	Eckfeld	Wappler et al. (2012)	22	0.001	0	0	1	0	0	0	1	0	44.3
Ruta Sp.	Eckfeld	Wappler et al. (2012)	29	0.000	0	0	1	0	0	0	1	0	44.3
Rhodomyrtophyllum sinuatum	Messel	Wappler et al. (2012)	17	0.000	0	0	1	0	0	0	1	0	47.8

Symplocos incondita	EPWR1601	Currano et al. (2019)	10	0.000	0	0	1	0	0	0	1	0	49.1
Dicot sp. WW053	42403	Currano et al. (2010)	8	0.005	0	0	1	0	0	0	1	0	52.7
Plant Host 1	41352	Wilf et al. (2001)	2	0.005	NA	NA	NA	NA	NA	NA	NA	NA	53
Dicot sp. WW003	42384	Currano et al. (2008)	9	0.001	0	0	1	0	0	0	1	0	55.8
Browniea serrata	42042	Currano et al. (2008)	3	0.000	0	0	1	0	1	0	0	0	57.5
Davidia antiqua	42041	Currano et al. (2008)	5	0.002	0	0	1	0	0	0	1	0	58.9
Corylites hebridicus	Kolfjellet	Wappler & Denk (2011)	6	0.010	0	0	1	0	0	0	1	0	61
FU7	441	Labandeira et al. (2002)	1	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.6
FU16	87150	Labandeira et al. (2002)	4	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.6
HC43	517	Labandeira et al. (2002)	2	0.002	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC212	567	Labandeira et al. (2002)	5	0.001	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC212	1491	Labandeira et al. (2002)	3	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC200	1781	Labandeira et al. (2002)	4	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC212	2203	Labandeira et al. (2002)	5	0.008	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC73	86102	Labandeira et al. (2002)	3	0.001	NA	NA	NA	NA	NA	NA	NA	NA	66.5

HC66	86153	Labandeira et al. (2002)	4	0.003	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC36	87129	Labandeira et al. (2002)	4	0.009	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC57	88111	Labandeira et al. (2002)	3	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
D80	302	This study	3	0.003	NA	NA	NA	NA	NA	NA	NA	NA	74.3
F10	9726	This study	10	0.003	NA	NA	NA	NA	NA	NA	NA	NA	74.3
sp25.1	Lost Valley	This study	7	0.001	NA	NA	NA	NA	NA	NA	NA	NA	75.6

Supplementary Table 6.2: Plant hosts with significantly lower levels of insect herbivory than expected and all relevant associated data.

Species/ Morpho-type	Locality	Pub-lication	Abun-dance Rank	p-value	Pterido-sperm	Gymno-sperm	Angio-sperm	ANA-Grade	Mag-nolii d	Mono-cot	Eu-dicot	N-Fix	Age (Ma)
Sorbus domestica	Bernasso	Adroit et al. (2016)	7	0.000	0	0	1	0	0	0	1	0	2
Acer opulifolium	Bernasso	Adroit et al. (2016)	11	0.000	0	0	1	0	0	0	1	0	2
Acer sp.	Bernasso	Adroit et al. (2016)	15	0.000	0	0	1	0	0	0	1	0	2
Fagus attenuata	Berga	Adroit et al. (2018)	1	0.004	0	0	1	0	0	0	1	0	2.8
Zelkova ungeri	Willershausen	Adroit et al. (2018)	1	0.000	0	0	1	0	0	0	1	0	2.8
Carpinus betulus	Willershausen	Adroit et al. (2018)	9	0.000	0	0	1	0	0	0	1	0	2.8
Oleaceae	Willershausen	Adroit et al. (2018)	18	0.006	0	0	1	0	0	0	1	0	2.8
Betula lenta	Willershausen	Adroit et al. (2018)	30	0.002	0	0	1	0	0	0	1	0	2.8
Ericaceae	Willershausen	Adroit et al. (2018)	76	0.000	0	0	1	0	0	0	1	0	2.8
Betulaceae	Willershausen	Adroit et al. (2018)	102	0.002	0	0	1	0	0	0	1	0	2.8
Buxaceae	Willershausen	Adroit et al. (2018)	105	0.000	0	0	1	0	0	0	1	0	2.8
Potamogeto sp.	Willershausen	Adroit et al. (2018)	109	0.000	0	0	1	0	0	1	0	0	2.8
Potamogeton crispus	Willershausen	Adroit et al. (2018)	115	0.000	0	0	1	0	0	0	0	0	2.8
Acer askelssonii	Brekkuá	Wappler & Grímsson	3	0.000	0	0	1	0	0	0	1	0	6.5

		(2016)											
Acer askelssonii	Mókollsdalur	Wappler & Grímsson (2016)	7	0.000	0	0	1	0	0	0	1	0	8.5
Acer islandicum	Mókollsdalur	Wappler & Grímsson (2016)	8	0.000	0	0	1	0	0	0	1	0	8.5
Ulmus sp.	Mókollsdalur	Wappler & Grímsson (2016)	9	0.000	0	0	1	0	0	0	1	0	8.5
Acer sp.	Tröllatunga	Wappler & Grímsson (2016)	4	0.000	0	0	1	0	0	0	1	0	10
Juglandaceae sp.	Tröllatunga	Wappler & Grímsson (2016)	5	0.000	0	0	1	0	0	0	1	0	10
Acer askelssonii	Brjánslækur (Barðaströnd)	Wappler & Grímsson (2016)	3	0.000	0	0	1	0	0	0	1	0	12
Morph 10	Hindon Maar	Möller et al. (2017)	7	0.000	NA	NA	NA	NA	NA	NA	NA	NA	18.8
Ripogonum	Hindon Maar	Möller et al. (2017)	12	0.001	0	0	1	0	0	1	0	0	18.8
Morph 6	Hindon Maar	Möller et al. (2017)	15	0.009	NA	NA	NA	NA	NA	NA	NA	NA	18.8
Monocot	Hindon Maar	Möller et al. (2017)	16	0.001	0	0	1	0	0	1	0	0	18.8
Daphnogene polymorpha	Břešťany	Knor et al. (2012)	2	0.004	0	0	1	0	1	0	0	0	19.6
Nyssa haidingeri	Břešťany	Knor et al. (2012)	6	0.005	0	0	1	0	0	0	1	0	19.6

Zelkova zelkovifolia	Břešťany	Knor et al. (2012)	17	0.000	0	0	1	0	0	0	1	0	19.6
Carya sp.	Břešťany	Knor et al. (2012)	20	0.000	0	0	1	0	0	0	1	0	19.6
Ulmus pyramidalis	Bílina	Knor et al. (2012)	2	0.003	0	0	1	0	0	0	1	0	19.6
Comptonia difformis	Bílina	Knor et al. (2012)	15	0.000	0	0	1	0	0	0	1	1	19.6
Rosa europaea	Bílina	Knor et al. (2012)	30	0.008	0	0	1	0	0	0	1	0	19.6
Crataegus sp.	Bílina	Knor et al. (2012)	59	0.000	0	0	1	0	0	0	1	0	19.6
Magnoliopsida sp. 2	Wappler (2010)	Orsberg	6	0.000	0	0	1	0	0	0	0	0	23
Magnoliopsida sp. 2	Wappler (2010)	Rott	1	0.000	0	0	1	0	0	0	0	0	23
Daphnogene cinnamomifolia	Wappler (2010)	Rott	4	0.000	0	0	1	0	1	0	0	0	23
Ailanthus ailanthifolia	Wappler (2010)	Rott	19	0.008	0	0	1	0	0	0	1	0	23
Juglandaceae	Wappler (2010)	Rott	31	0.000	0	0	1	0	0	0	1	0	23
Laurus obovata	Wappler (2010)	Rott	36	0.000	0	0	1	0	0	0	0	0	23
Trigonobalanopsis rhamnoides	Wappler (2010)	Rott	37	0.000	0	0	1	0	0	0	1	0	23
Eotrigonobalanus furcinervis	Wappler (2010)	Rott	47	0.000	0	0	1	0	0	0	1	0	23

Fagus deucalionis	Wappler (2010)	Rott	54	0.000	0	0	1	0	0	0	1	0	23
Vacciniu m rottense	Wappler (2010)	Rott	59	0.000	0	0	1	0	0	0	1	0	23
Daphnoge ne sp.	Enspel	Gunkel et al. (2015)	6	0.010	0	0	1	0	1	0	0	0	24.8
Daphnoge ne cinnamom ifolia	Enspel	Gunkel et al. (2015)	17	0.000	0	0	1	0	1	0	0	0	24.8
Cupressac eae	Domíngue z (2018)	Level NH	2	0.000	0	1	0	0	0	0	0	0	25.4
Liquidam bar europaea	Quegstein	Wappler (2010)	6	0.000	0	0	1	0	0	0	1	0	25.8
Magnolia attenuata	Quegstein	Wappler (2010)	7	0.000	0	0	1	0	0	0	0	0	25.8
Laurophyl lum sp.	Quegstein	Wappler (2010)	8	0.000	0	0	1	0	0	0	0	0	25.8
Albizia	CH72	Currano et al. (2011)	1	0.001	0	0	1	0	0	0	1	1	27.5
Mildbrae diodendro n	CH72	Currano et al. (2011)	9	0.000	0	0	1	0	0	0	1	1	27.5
Morphoty pe 13	323	Wilf et al. (2001)	1	0.000	NA	NA	NA	NA	NA	NA	NA	NA	43
Morphoty pe 13	1732	Wilf et al. (2001)	1	0.000	NA	NA	NA	NA	NA	NA	NA	NA	43
Morphoty pe 5	1732	Wilf et al. (2001)	6	0.000	NA	NA	NA	NA	NA	NA	NA	NA	43
Morphoty pe 28	1732	Wilf et al. (2001)	11	0.000	NA	NA	NA	NA	NA	NA	NA	NA	43
Fagales sp.	Nathorstfj ellet	Wappler & Denk (2011)	9	0.000	0	0	1	0	0	0	1	0	44
Trochode ndroides	Nathorstfj ellet	Wappler & Denk	11	0.000	0	0	1	0	0	0	1	0	44

crenulata		(2011)											
Apocy Sp.	Eckfeld	Wappler et al. (2012)	2	0.000	0	0	1	0	0	0	1	0	44.3
Tern. Dent.	Eckfeld	Wappler et al. (2012)	3	0.000	NA	NA	NA	NA	NA	NA	NA	NA	44.3
Pungi. Walt.	Eckfeld	Wappler et al. (2012)	4	0.000	0	0	1	0	1	0	0	0	44.3
Dicot Ulmo	Eckfeld	Wappler et al. (2012)	5	0.000	0	0	1	0	0	0	1	0	44.3
Carp. Sp.	Eckfeld	Wappler et al. (2012)	7	0.000	0	0	1	0	0	0	1	0	44.3
Faba Typ1	Eckfeld	Wappler et al. (2012)	8	0.000	0	0	1	0	0	0	1	1	44.3
Compt Sp.	Eckfeld	Wappler et al. (2012)	12	0.000	0	0	1	0	0	0	1	1	44.3
Cerci Sp.	Eckfeld	Wappler et al. (2012)	15	0.004	0	0	1	0	0	0	1	0	44.3
Myricac Sp.	Eckfeld	Wappler et al. (2012)	16	0.006	0	0	1	0	0	0	1	1	44.3
Poly Sp.	Eckfeld	Wappler et al. (2012)	21	0.000	0	0	1	0	0	0	1	0	44.3
Ulmus Sp.	Eckfeld	Wappler et al. (2012)	23	0.000	0	0	1	0	0	0	1	0	44.3
Zelko Sp.	Eckfeld	Wappler et al. (2012)	25	0.000	0	0	1	0	0	0	1	0	44.3
Thea Sp.	Eckfeld	Wappler et al.	28	0.000	0	0	1	0	0	0	1	0	44.3

		(2012)											
Daph Sp.	Eckfeld	Wappler et al. (2012)	31	0.000	0	0	1	0	1	0	0	0	44.3
Myri Sp.	Eckfeld	Wappler et al. (2012)	32	0.000	0	0	1	0	0	0	1	1	44.3
Laurophyllum lanigeroides	Messel	Wappler et al. (2012)	2	0.000	0	0	1	0	0	0	0	0	47.8
Daphnogene crebrigranosa	Messel	Wappler et al. (2012)	8	0.000	0	0	1	0	1	0	0	0	47.8
Daphnogene sp.	Messel	Wappler et al. (2012)	9	0.011	0	0	1	0	1	0	0	0	47.8
Ulmaceae sp.	Messel	Wappler et al. (2012)	11	0.004	0	0	1	0	0	0	1	0	47.8
Daphnogene sp1	Messel	Wappler et al. (2012)	13	0.000	0	0	1	0	1	0	0	0	47.8
Dicot spGM002	Messel	Wappler et al. (2012)	14	0.000	0	0	1	0	0	0	1	0	47.8
Laurophyllum hirsutum	Messel	Wappler et al. (2012)	16	0.002	0	0	1	0	0	0	0	0	47.8
Nymphaeaceae sp.	Messel	Wappler et al. (2012)	19	0.000	0	0	1	0	0	0	0	0	47.8
Ulmoideae *Formenkreis* 1	Messel	Wappler et al. (2012)	21	0.000	0	0	1	0	0	0	1	0	47.8
Laurophyllum sp2	Messel	Wappler et al.	23	0.000	0	0	1	0	0	0	0	0	47.8

		(2012)											
Cercidiphyllum sp	Messel	Wappler et al. (2012)	28	0.000	0	0	1	0	0	0	1	0	47.8
Hedera sp	Messel	Wappler et al. (2012)	34	0.000	0	0	1	0	0	0	1	0	47.8
Juglandaceae Formenkreis 3	Messel	Wappler et al. (2012)	35	0.000	0	0	1	0	0	0	1	0	47.8
Laurophyllum natistomum	Messel	Wappler et al. (2012)	37	0.000	0	0	1	0	0	0	0	0	47.8
Laurophyllum tertiarium	Messel	Wappler et al. (2012)	38	0.000	0	0	1	0	0	0	0	0	47.8
Menispermaceae sp	Messel	Wappler et al. (2012)	39	0.000	0	0	1	0	0	0	1	0	47.8
Sloanea sp	Messel	Wappler et al. (2012)	40	0.001	0	0	1	0	0	0	1	0	47.8
Ternstroemites dentaus	Messel	Wappler et al. (2012)	41	0.003	0	0	1	0	0	0	1	0	47.8
Cabomba sp	Messel	Wappler et al. (2012)	48	0.000	0	0	1	1	0	0	0	0	47.8
Comptonia sp	Messel	Wappler et al. (2012)	49	0.000	0	0	1	0	0	0	1	1	47.8
Daphnogene cryptostoma	Messel	Wappler et al. (2012)	50	0.000	0	0	1	0	1	0	0	0	47.8
Daphnogene	Messel	Wappler et al.	51	0.000	0	0	1	0	1	0	0	0	47.8

leptohuephe		(2012)											
Daphnogene multipora	Messel	Wappler et al. (2012)	52	0.000	0	0	1	0	1	0	0	0	47.8
Laurophyllum glaphyre	Messel	Wappler et al. (2012)	53	0.000	0	0	1	0	0	0	0	0	47.8
Laurophyllum sp1	Messel	Wappler et al. (2012)	54	0.000	0	0	1	0	0	0	0	0	47.8
Polyspora hassiaca	Messel	Wappler et al. (2012)	55	0.000	0	0	1	0	0	0	1	0	47.8
Symplocos sp	Messel	Wappler et al. (2012)	56	0.000	0	0	1	0	0	0	1	0	47.8
Ampelopsis sp	Messel	Wappler et al. (2012)	59	0.000	0	0	1	0	0	0	1	0	47.8
Byttneriophyllum tiliaefolium	Messel	Wappler et al. (2012)	66	0.000	0	0	1	0	0	0	1	0	47.8
Daphnogene eocaenica	Messel	Wappler et al. (2012)	67	0.000	0	0	1	0	1	0	0	0	47.8
Daphnogene sp3	Messel	Wappler et al. (2012)	68	0.000	0	0	1	0	1	0	0	0	47.8
Laurophyllum alatum	Messel	Wappler et al. (2012)	70	0.000	0	0	1	0	0	0	0	0	47.8
Laurophyllum ebenoides	Messel	Wappler et al. (2012)	71	0.000	0	0	1	0	0	0	0	0	47.8
Laurophyllum lutetium	Messel	Wappler et al. (2012)	72	0.000	0	0	1	0	0	0	0	0	47.8

Laurophyllum schottleri	Messel	Wappler et al. (2012)	74	0.000	0	0	1	0	0	0	0	0	47.8
Laurophyllum streble	Messel	Wappler et al. (2012)	75	0.000	0	0	1	0	0	0	0	0	47.8
Laurophyllum weylandii	Messel	Wappler et al. (2012)	76	0.000	0	0	1	0	0	0	0	0	47.8
Leguminosae sp2	Messel	Wappler et al. (2012)	78	0.000	0	0	1	0	0	0	1	1	47.8
Leguminosae sp3	Messel	Wappler et al. (2012)	79	0.000	0	0	1	0	0	0	1	1	47.8
Leguminosae sp4	Messel	Wappler et al. (2012)	80	0.000	0	0	1	0	0	0	1	1	47.8
Platanus fraxinifolia	Messel	Wappler et al. (2012)	81	0.000	0	0	1	0	0	0	1	0	47.8
Viscophyllum pinnatum	Messel	Wappler et al. (2012)	84	0.000	0	0	1	0	0	0	1	0	47.8
Viscophyllum septemnervium	Messel	Wappler et al. (2012)	85	0.000	0	0	1	0	0	0	1	0	47.8
Dicot sp. AY004	EPWR1601	Currano et al. (2019)	5	0.000	0	0	1	0	0	0	1	0	49.1
Platanites raynoldsii	EPWR1601	Currano et al. (2019)	9	0.000	0	0	1	0	0	0	1	0	49.1
Aleurites fremontensis	EPWR1601	Currano et al. (2019)	11	0.000	0	0	1	0	0	0	1	0	49.1
Dicot sp. AY008	EPWR1601	Currano et al. (2019)	12	0.000	0	0	1	0	0	0	1	0	49.1

Aleurites fremontensis	EPWR1602	Currano et al. (2019)	6	0.000	0	0	1	0	0	0	1	0	49.1
Platanites raynoldsii	EPWR1602	Currano et al. (2019)	7	0.000	0	0	1	0	0	0	1	0	49.1
Dicot sp. AY005	EPWR1602	Currano et al. (2019)	8	0.000	0	0	1	0	0	0	1	0	49.1
Symplocos incondita	EPWR1602	Currano et al. (2019)	10	0.000	0	0	1	0	0	0	1	0	49.1
Dicot sp. AY009	EPWR1603	Currano et al. (2019)	2	0.000	0	0	1	0	0	0	1	0	49.1
Dicot sp. AY005	EPWR1603	Currano et al. (2019)	8	0.000	0	0	1	0	0	0	1	0	49.1
Platanites raynoldsii	EPWR1603	Currano et al. (2019)	9	0.000	0	0	1	0	0	0	1	0	49.1
Aleurites fremontensis	EPWR1603	Currano et al. (2019)	11	0.000	0	0	1	0	0	0	1	0	49.1
Dicot sp. AY009	EPWR1604	Currano et al. (2019)	4	0.000	0	0	1	0	0	0	1	0	49.1
Dicot sp. WR007	EPWR1604	Currano et al. (2019)	7	0.000	0	0	1	0	0	0	1	0	49.1
Dicot sp. AY004	EPWR1604	Currano et al. (2019)	8	0.000	0	0	1	0	0	0	1	0	49.1
Symplocos incondita	DMNH5102	Currano et al. (2019)	1	0.000	0	0	1	0	0	0	1	0	52.4
Dicot sp. WR007	DMNH5102	Currano et al. (2019)	8	0.000	0	0	1	0	0	0	1	0	52.4

Dicot sp. WW052	42402	Currano et al. (2010)	3	0.001	0	0	1	0	0	0	1	0	52.7
"Dombeya" novi-mundi	42403	Currano et al. (2010)	4	0.005	0	0	1	0	0	0	1	0	52.7
Morphotype 18	41342	Wilf et al. (2001)	2	0.004	NA	NA	NA	NA	NA	NA	NA	NA	53
Morphotype 3	41352	Wilf et al. (2001)	1	0.000	NA	NA	NA	NA	NA	NA	NA	NA	53
Fabaceae sp. WW040	37560	Currano et al. (2010)	2	0.000	0	0	1	0	0	0	1	1	53.4
Fabaceae sp. WW042	37560	Currano et al. (2010)	5	0.008	0	0	1	0	0	0	1	1	53.4
dicot sp. WW001	42384	Currano et al. (2008)	1	0.000	0	0	1	0	0	0	1	0	55.8
Platanus raynoldsi	41643	Currano et al. (2008)	4	0.000	0	0	1	0	0	0	1	0	55.9
Morphotype 8	41270	Wilf et al. (2001)	1	0.007	NA	NA	NA	NA	NA	NA	NA	NA	56
Platanus raynoldsi	42411	Currano et al. (2010)	5	0.000	0	0	1	0	0	0	1	0	56.4
Persites argutus	42042	Currano et al. (2008)	1	0.000	0	0	1	0	1	0	0	0	57.5
Browniea serrata	42041	Currano et al. (2008)	2	0.008	0	0	1	0	1	0	0	0	58.9
Platanus raynoldsi	42041	Currano et al. (2008)	3	0.001	0	0	1	0	0	0	1	0	58.9
HB182	A	Schmidt et al. (2019)	2	0.000	NA	NA	NA	NA	NA	NA	NA	NA	59.5

HB178	A	Schmidt et al. (2019)	5	0.000	NA	NA	NA	NA	NA	NA	NA	NA	59.5
"Cinnamomum" martyi	Menat	Wappler et al. (2009)	7	0.010	0	0	1	0	1	0	0	0	60.5
"Corylus" sp.	Menat	Wappler et al. (2009)	12	0.000	0	0	1	0	0	0	1	0	60.5
"Atriplex" borealis	Menat	Wappler et al. (2009)	22	0.000	0	0	1	0	0	0	1	0	60.5
Acer arcticum	Kolfjellet	Wappler & Denk (2011)	10	0.000	0	0	1	0	0	0	1	0	61
SA73	LF	Donovan et al. (2018)	2	0.008	NA	NA	NA	NA	NA	NA	NA	NA	62.4
SA43	PL2	Donovan et al. (2018)	6	0.008	NA	NA	NA	NA	NA	NA	NA	NA	64.1
SA47	PL2	Donovan et al. (2018)	8	0.000	NA	NA	NA	NA	NA	NA	NA	NA	64.1
SA16	PL2	Donovan et al. (2018)	9	0.010	NA	NA	NA	NA	NA	NA	NA	NA	64.1
SA8	PL2	Donovan et al. (2018)	14	0.001	NA	NA	NA	NA	NA	NA	NA	NA	64.1
SA58	PL2	Donovan et al. (2018)	18	0.004	NA	NA	NA	NA	NA	NA	NA	NA	64.1
SA50	PL2	Donovan et al. (2018)	19	0.004	NA	NA	NA	NA	NA	NA	NA	NA	64.1
SA44	PL1	Donovan et al. (2018)	6	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.22

SA8	PL1	Donovan et al. (2018)	9	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.22
SA5	PL1	Donovan et al. (2018)	14	0.003	NA	NA	NA	NA	NA	NA	NA	NA	65.22
FU7	562	Labandeira et al. (2002)	4	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.6
FU2	2217	Labandeira et al. (2002)	3	0.003	NA	NA	NA	NA	NA	NA	NA	NA	65.6
HC123	2217	Labandeira et al. (2002)	8	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.6
FU38	86107	Labandeira et al. (2002)	3	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.6
FU35	86107	Labandeira et al. (2002)	8	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.6
FU3	86110	Labandeira et al. (2002)	2	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.6
FU4	86110	Labandeira et al. (2002)	3	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.6
FU4	87150	Labandeira et al. (2002)	1	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.6
FU26	87150	Labandeira et al. (2002)	2	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.6
FU51	87150	Labandeira et al. (2002)	5	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.6
FU3	88103	Labandeira et al. (2002)	1	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.6

FU26	88103	Labandeira et al. (2002)	2	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.6
FU1	88103	Labandeira et al. (2002)	6	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.6
FU4	KJ8403	Labandeira et al. (2002)	2	0.000	NA	NA	NA	NA	NA	NA	NA	NA	65.6
Morphotype 20	LefE	Donovan et al. (2018)	9	0.010	NA	NA	NA	NA	NA	NA	NA	NA	66.5
Morphotype 36	LefE	Donovan et al. (2018)	16	0.005	NA	NA	NA	NA	NA	NA	NA	NA	66.5
Morphotype 61	LefE	Donovan et al. (2018)	20	0.003	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC166	428	Labandeira et al. (2002)	1	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC165	428	Labandeira et al. (2002)	10	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC180	428	Labandeira et al. (2002)	16	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
Taxodiaceae	428	Labandeira et al. (2002)	21	0.000	0	1	0	0	0	0	0	0	66.5
HC62	517	Labandeira et al. (2002)	4	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC165	517	Labandeira et al. (2002)	6	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC200	517	Labandeira et al. (2002)	7	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5

HC44	517	Labandeira et al. (2002)	8	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC32	566	Labandeira et al. (2002)	2	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC103	566	Labandeira et al. (2002)	4	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC80	567	Labandeira et al. (2002)	2	0.002	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC137	567	Labandeira et al. (2002)	8	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
Taxodiaceae	567	Labandeira et al. (2002)	9	0.000	0	1	0	0	0	0	0	0	66.5
HC225	567	Labandeira et al. (2002)	11	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC70	567	Labandeira et al. (2002)	12	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC103	568	Labandeira et al. (2002)	3	0.002	NA	NA	NA	NA	NA	NA	NA	NA	66.5
Taxodiaceae	571	Labandeira et al. (2002)	3	0.000	0	1	0	0	0	0	0	0	66.5
FU4	571	Labandeira et al. (2002)	5	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC71	571	Labandeira et al. (2002)	7	0.004	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC71	897	Labandeira et al. (2002)	3	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5

FU37	900	Labandeira et al. (2002)	6	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC111	900	Labandeira et al. (2002)	17	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC135	1491	Labandeira et al. (2002)	1	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC211	1491	Labandeira et al. (2002)	4	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC90	1491	Labandeira et al. (2002)	6	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
Taxodiaceae	1491	Labandeira et al. (2002)	7	0.000	0	1	0	0	0	0	0	0	66.5
HC165	1781	Labandeira et al. (2002)	1	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC70	1781	Labandeira et al. (2002)	6	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC49	1855	Labandeira et al. (2002)	2	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC241	2087	Labandeira et al. (2002)	2	0.001	NA	NA	NA	NA	NA	NA	NA	NA	66.5
Morph-E	2087	Labandeira et al. (2002)	10	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
Taxodiaceae	2097	Labandeira et al. (2002)	6	0.000	0	1	0	0	0	0	0	0	66.5
HC266	2098	Labandeira et al. (2002)	1	0.001	NA	NA	NA	NA	NA	NA	NA	NA	66.5

FU2	2098	Labandeira et al. (2002)	2	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC81	86100	Labandeira et al. (2002)	1	0.006	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC80	86100	Labandeira et al. (2002)	2	0.010	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC35	86100	Labandeira et al. (2002)	5	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC90	86100	Labandeira et al. (2002)	9	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
Taxodiaceae	86100	Labandeira et al. (2002)	11	0.000	0	1	0	0	0	0	0	0	66.5
HC71	86102	Labandeira et al. (2002)	4	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC70	86102	Labandeira et al. (2002)	5	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
FU37	86102	Labandeira et al. (2002)	9	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC1	87110	Labandeira et al. (2002)	3	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC44	87110	Labandeira et al. (2002)	5	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC57	87129	Labandeira et al. (2002)	5	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
Taxodiaceae	87134	Labandeira et al. (2002)	4	0.000	0	1	0	0	0	0	0	0	66.5

FU3	87134	Labandeira et al. (2002)	5	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
Taxodiaceae	88111	Labandeira et al. (2002)	1	0.000	0	1	0	0	0	0	0	0	66.5
HC114	88111	Labandeira et al. (2002)	2	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
HC32	88111	Labandeira et al. (2002)	4	0.000	NA	NA	NA	NA	NA	NA	NA	NA	66.5
D2	302	This study	1	0.000	NA	NA	NA	NA	NA	NA	NA	NA	74.3
C10	9726	This study	1	0.000	NA	NA	NA	NA	NA	NA	NA	NA	74.3
D45	9726	This study	4	0.000	NA	NA	NA	NA	NA	NA	NA	NA	74.3
D29	9726	This study	6	0.000	NA	NA	NA	NA	NA	NA	NA	NA	74.3
M3	9726	This study	9	0.000	NA	NA	NA	NA	NA	NA	NA	NA	74.3
Morphotype 33.2	Caveat Friendship	This study	1	0.011	NA	NA	NA	NA	NA	NA	NA	NA	75.6
Morphotype 17.1	Caveat Friendship	This study	3	0.000	NA	NA	NA	NA	NA	NA	NA	NA	75.6
Morphotype 12.1	Caveat Friendship	This study	5	0.001	NA	NA	NA	NA	NA	NA	NA	NA	75.6
Morphotype 7.1	Caveat Friendship	This study	9	0.000	NA	NA	NA	NA	NA	NA	NA	NA	75.6
Morphotype 10.2	Caveat Friendship	This study	11	0.000	NA	NA	NA	NA	NA	NA	NA	NA	75.6
Morphotype 10.3	Caveat Friendship	This study	12	0.000	NA	NA	NA	NA	NA	NA	NA	NA	75.6
Morphotype 24.2	Caveat Friendship	This study	14	0.005	NA	NA	NA	NA	NA	NA	NA	NA	75.6
Morphotype 11.1	Caveat Friendship	This study	15	0.000	NA	NA	NA	NA	NA	NA	NA	NA	75.6
Morphoty	Caveat	This	19	0.00	NA	NA	NA	NA	NA	NA	NA	N	75.6

pe 10.4	Friendship	study		0								A	
Morphotype 29.1	Caveat Friendship	This study	20	0.000	NA	NA	NA	NA	NA	NA	NA	NA	75.6
Morphotype 31.1	Caveat Friendship	This study	21	0.000	NA	NA	NA	NA	NA	NA	NA	NA	75.6
sp35.1	Lost Valley	This study	5	0.003	NA	NA	NA	NA	NA	NA	NA	NA	75.6
sp31.4	Lost Valley	This study	6	0.002	NA	NA	NA	NA	NA	NA	NA	NA	75.6
sp31.2	Lost Valley	This study	8	0.000	NA	NA	NA	NA	NA	NA	NA	NA	75.6
sp11.2	Lost Valley	This study	15	0.001	NA	NA	NA	NA	NA	NA	NA	NA	75.6
sp30.2	Lost Valley	This study	20	0.002	NA	NA	NA	NA	NA	NA	NA	NA	75.6
sp7.6	Lost Valley	This study	24	0.000	NA	NA	NA	NA	NA	NA	NA	NA	75.6
sp7.4	Lost Valley	This study	28	0.000	NA	NA	NA	NA	NA	NA	NA	NA	75.6
sp5.1	Lost Valley	This study	33	0.000	NA	NA	NA	NA	NA	NA	NA	NA	75.6
sp39.1	JARS	This study	2	0.001	NA	NA	NA	NA	NA	NA	NA	NA	75.7
sp7.1	JARS	This study	4	0.000	NA	NA	NA	NA	NA	NA	NA	NA	75.7
sp12.1	JARS	This study	5	0.008	NA	NA	NA	NA	NA	NA	NA	NA	75.7
sp5.1	JARS	This study	13	0.001	NA	NA	NA	NA	NA	NA	NA	NA	75.7

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